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October 1912

Editor: JOHN M. COULTER

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THE

BOTANICAL GAZETTE

OCTOBER 1912

COMPARATIVE ANATOMY OF DUNE PLANTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 161

ANNA M. STARR

(WITH THIRTY-FIVE FIGURES)

The literature of ecological anatomy is extensive when one considers that the whole subject of ecology is a late arrival in the field of botany. Comparative anatomy, ecologically viewed, is limited enough to justify a brief review. BONNIER (1) was a pioneer in experimental work, taking parts of plants growing in intermediate situations in the mountains and transplanting one part to the lowlands and another part to alpine conditions. He found that the plants grown in the two habitats differed in appearance, habit, and structure (2). GREVILLIUS (15) in an extensive work on the island Öland compared the vegetation of the alvar, a dry, rocky, treeless plain, with that of the fertile regions. CHRYSLER (7) compared the anatomy of strand plants at Woods Hole with that of the same species growing on the shores of Lake Michigan. CANNON (5) at the Desert Laboratory (Tucson) contributed some experiments on desert plants, keeping some plants under irrigation and letting others of the same species grow without irrigation, his study being a comparison of the conductive tissues. CHERMEZON (6) in a recent contribution to the anatomy of littoral vegetation makes some comparison of it with that of continental plants. All agree that the structure of plants varies with change in conditions.

In 1899 COWLES (8) published the results of his studies of the sand dunes of Lake Michigan, describing the general features of

the coast, the ecological factors, and the plant associations. It was his intention to enter into an investigation of the anatomical relations of the plants described, but other work prevented. In the fall of 1908 he suggested that I undertake the study, and it has been under his direction that the work has been carried on. I wish to express my grateful thanks to him and to all the members of the Department who helped me with criticism and advice, and also to those who aided me in photographic work and in collecting material. In 1904 C. L. HOLTZMAN, in an unpublished dissertation, described the leaves of six of the species included in my work, and I have had access to his paper.

The dune plants were collected from the Indiana dunes, chiefly from the vicinity of Miller's, Dune Park, and Furnessville. The mesophytic forms came mainly from the flood plains of the Desplaines River at Riverside; some were collected in other mesophytic woods in the same general locality, while a few came from the Mississippi flood plain.

The stems and roots were preserved in formalin and 50 per cent alcohol and cut with a hand microtome. The leaves that made the most successful permanent preparations were killed with corrosive sublimate dissolved in 95 per cent alcohol, used hot. These were easily sectioned in paraffin. I found 8 μ the most satisfactory thickness. Free-hand sections were also made. Safranin and anilin blue were used in staining. The names are those given in the seventh edition of GRAY'S *Manual* and differ therefore at times from those used by COWLES. The drawings were made by the aid of a camera lucida, magnified 470 diameters, and reduced one-half in reproduction.

Ecological factors in the dunes

LIGHT AND HEAT.—There is direct illumination, increased by reflection from the sand. Because of the scanty vegetation and the great exposure, the temperature of the air is higher in summer and lower in winter than in more protected localities. Owing to the high conductivity of sand, the same great divergence between extremes is present in the temperature of the soil.

WIND.—COWLES considers this the most potent factor in determining the character of the dune vegetation. The winds

gather force as they sweep across the lake, and when they reach the shore they gather up sand and carry it along with a force that carves and scars the bark of the trees on the windward side or completely wears it away, as in the case of *Cornus stolonifera*.

SOIL.—The soil is chiefly quartz sand, the particles being relatively large, so that it is extremely porous, which has a great influence on the water and heat relations. As a rule sandy soils are poor in nutrient food materials, nor do they rapidly develop a rich humus because of the rapid oxidation of the organic matter.

WATER.—The surface layer of soil is very dry, as the capillarity of sand is less than that of other soils, evaporation from a sandy surface is rapid, and precipitated water percolates quickly, the water capacity of sand being slight. On the other hand, a sandy soil yields its water to plants more freely than other soils, and below the superficial layer of dry sand there is always a surprising amount of water. FULLER (**13**) has found this to be more than double the wilting coefficient of dune soil.

BIOTIC FACTORS.—The only biotic factors of marked influence in the dunes are those associated with the plants themselves when they are once established, humus and shade. Humus influences the temperature of the soil and increases the water content, the number of soil organisms, toxicity, and aeration. Shade influences the germination of seeds and increases the accumulation of humus and atmospheric humidity, and so decreases evaporation. FULLER (**12**) finds that in the cottonwood dunes the evaporation is 21 cc. per day, while on the pine dunes it is 11 cc., in the oak dunes 10 cc., and in the beech-maple forest 8 cc., a descending scale from the pioneer formation to the climax forest.

Description of the plants

I. XEROPHYTIC FORMS

Herbs

Cakile edentula.—A small, very succulent annual. Leaves smooth and thick; outer walls of epidermis 4 μ; several rows of palisade on each side with a narrow zone of sponge in the center; water-storage tissue about the bundles; stomata on both surfaces; conductive elements not well developed. Stem with epidermal walls thickened all around, the outer 10 μ.

Euphorbia polygonifolia.—A little prostrate succulent annual with abundant latex. Leaves small, thick, inclined to be folded at right angles on the midrib; walls of epidermis thickened, outer 9–12 μ on the upper surface and 15 μ at the edges of the leaf; stomata sunken to the depth of the epidermis; a layer of palisade cells next the upper epidermis and "festoon" palisade about the bundles; a layer of water-storage tissue next the lower epidermis; cells at the bend of the midrib collenchymatous; small development of vascular elements. Stem woody for so small a plant, having a compact vascular cylinder; walls of epidermis thick, outer 8 μ, cuticle 4.6 μ; cells below thickened; latex tubes conspicuous.

Corispermum hyssopifolium.—Low, branching, succulent annual. Leaf thick, narrow, linear; two layers of palisade on both sides and water-storage tissue in the center; walls of the epidermis thickened, outer 16 μ; cells with thickened walls about the midrib at the edges of the leaf. Stem with two layers of palisade in the cortex and collenchyma at the surface; walls of epidermis heavy, outer 9.6 μ. Root sclerenchymatous except a few outer layers.

Artemisia caudata and *A. canadensis.*—Stout, bushy biennials or perennials. Leaf divided, divisions thick, smallest almost cylindrical, generally pubescent; double row of palisade on both surfaces, water-storage tissue inside; walls of epidermis thickened, outer wall 6–11 μ; stomata sunken one-half the depth of the epidermal cells. Stem with pith rapidly reduced after the first year, small in older, a dense cylinder of wood extending almost to the center; great masses of fibers capping the phloem; outer layers of cortex collenchymatous; considerable cork.

Cirsium Pitcheri.—Biennial, tomentose. Leaf very thick, with revolute margins; epidermal cells small, with thickened walls, outer 6.4 μ; chlorophyll confined to 2–4 outer layers of cells; the rest water-storage tissue with cells increasing in size toward the center with large air spaces between. Stem generally hollow, cortex thick, bundles few, with large vessels and masses of heavy fibers; rays wider than the bundles, the cells with thickened walls, outer cells of cortex collenchymatous.

Lathyrus maritimus.—A smooth trailing perennial herb. Leaf with palisade occupying almost half of the mesophyll, the sponge tissue rather compact; fibers above and below the bundles. Stem sharply angled; phloem capped by a heavy crescent of sclerenchyma; a second ring of sclerenchyma penetrating a distance between the bundles; medullary rays thin; outer wall of epidermis 6.2 μ. Root with large vessels; about one-half the pith made up of scattered masses of sclerenchyma.

Ammophila arenaria.—A stout perennial grass with firm creeping rootstocks that anchor the dunes. Leaf with morphologically upper surface rolled in; the surface a series of ridges and grooves; bundles under the ridges; edges of the leaf and ridges strengthened with hypodermal sclerenchyma, that in the ridges extending into the bundles; upper epidermal cells large and globular, or prolonged into conical hairs; stomata on the upper surface sunken to the depth of the epidermal cells; chlorenchyma reduced to strands each side the bundles; air spaces very small; outer wall of the lower epidermis (the exposed side) 6.4 μ thick, the cuticle 3.2 μ. Stem with cortical tissue sclerenchymatous; walls of the epidermis slightly thickened all around.

Andropogon scoparius (bunch-grass).—Leaf stiffened with a series of bundles, large ones alternating with three small ones, the space above the small ones filled in with three or four enormous epidermal cells and smaller, hypodermal, colorless cells; epidermal cells occasionally prolonged into sharp hairs, longer than those of *Ammophila;* the large cells collapse at the bend of the leaf, as it folds with the upper surface in; masses of sclerenchyma above and below the large bundles and below the middle of the small ones; chlorenchyma above the bundles; outer wall 9.3 μ; cuticle, thick; stomata on lower surface not sunken.

Calamovilfa longifolia.—A rigid perennial grass with horizontal rootstocks and pubescent sheaths; another dune former. Leaf with lower surface plane; with ridges and narrow depressions on the upper surface which rolls in as in *Ammophila;* walls of epidermis thick, cuticle thick; bundles in the ridges with sclerenchyma above and below, and sometimes about the phloem; hypodermal sclerenchyma next to the lower surface and at the top of the ridges; short,

pointed hairs on the upper surface; chlorenchyma, a layer of palisade, and a layer of spherical cells about the bundles; walls of parenchyma cells sometimes folded in as in *Pinus;* stomata sunken as in *Ammophila.* Stem with bundles more numerous toward the periphery, where the cells of the fundamental tissue become smaller; epidermal cells very small.

Solidago racemosa Gillmani (fig. 1).—A perennial herb, woody at the base. Leaf with outer wall of lower epidermis 8 μ thick, cuticle 2.4 μ; chlorenchyma above and below; water-storage tissue in the center; chlorenchyma above scarcely palisade-like, but of two or more layers of slightly elongated cells forming a compact tissue; good development of bundles in the midrib. Stem with small pith; cortex thick, containing groups of fibers and occasionally sclereids, outer layers collenchymatous; crystals in the cells of the pith. Root with ground tissue of sclerenchyma; outer cells of cortex collenchymatous.

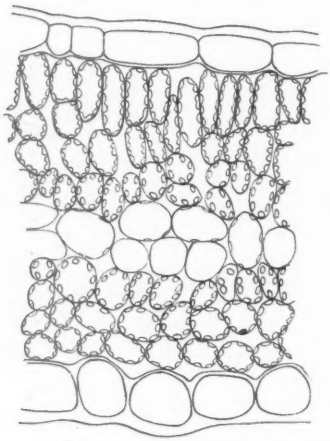


FIG. 1.—*Solidago racemosa Gillmani:* section of leaf.

Lithospermum Gmelini.—A perennial herb clothed with bristly hairs. Leaf thick, coarse, rough on both surfaces, with appressed hairs, bent upward at the midrib; outer wall of epidermis thick on both surfaces, 9.3 μ; palisade next both epidermal layers made up of a row of long cells, or of two rows of shorter cells; three layers in the center almost colorless; stomata not sunken. Stem with a small solid cylinder of wood made up chiefly of fibers, the vessels large; outer layers of cortex slightly collenchymatous; outer wall of epidermis 5 μ thick.

Arenaria stricta.—A low, tufted herb. Leaf smooth, needle-like; epidermal cells enormous, thickened on all sides especially at the edges of the leaf; outer wall 3.2–7 μ; cuticle thick; sclerenchyma below the bundles; whole mesophyll composed of compact tissue; no palisade; crystals frequent.

Opuntia Rafinesqui.—Stem doing the chlorophyll work; outer wall of epidermis 8 μ thick, cuticle 2.4 μ; several hypodermal layers of small heavy-walled cells; the chlorenchyma composed of many layers of cells elongated perpendicularly to the surface; the center of the stem occupied by a loose tissue of large colorless cells, the whole retaining water so effectually that it is difficult to dry it out even with heat and pressure; vascular system poorly developed; walls of the elements thin.

Shrubs

Prunus pumila.—A low shrub spreading easily in all directions and thus important in helping to make dunes stationary. Leaf thick, 216 μ; outer wall of epidermis 5–6 μ; cuticle very thick, ridged on the lower surface, the ridges so high that they fray out along the edge; cells above and below the midrib papillate and cuticle smooth, 8 μ; heavy masses of collenchyma above the stele of the midrib and several layers below, also in other large veins; great development of conductive elements; palisade double and festoon palisade above the bundles in the veins; lower cells of mesophyll palisade-like; crystals, oil, and other deposits abundant. Stem with vessels large and generally numerous; wood fibers heavy, with small lumen; groups of sclerenchyma in the cortex; cork thick.

Salix syrticola.—A shrub with the same habits as *Prunus pumila.* Leaf with upper surface silky, lower hairy, closely serrate, glandular; stipules large; outer wall of upper epidermis thick; heavy sclerenchyma above and below the stele of the midrib, and collenchyma next the epidermis on both sides; two layers of palisade next the upper epidermis and three more layers elongated vertically. Stem with medullary rays very narrow; vessels not large but numerous; fibers heavy, with small lumen; outer layer of pith sclerenchymatous; outer layers of cortex collenchymatous; three rows of mechanical fibers in the cortex, the outermost very wide.

Hudsonia tomentosa.—A bushy, heathlike shrub. Leaf small, awl-shaped, hairy on both surfaces and especially along the edges; upper epidermis composed of large cells; palisade about one-half the mesophyll of the narrow part of the leaf. Stem hairy, very woody, the vascular cylinder occupying most of the diameter, composed of very heavy fibers and few vessels; a few large scleren-

chymatous cells form the pith; a few rows of cells, part of them fibrous, form the cortex.

Arctostaphylos Uva-ursi.—A woody little plant trailing over the ground. Leaf thick, smooth, evergreen; outer wall of epidermis of both surfaces thick, cutinized; side walls plane, cutin sometimes 16 μ thick; upper epidermis sometimes divided periclinally; bundles compactly developed, with fibers above and below; collenchyma next the epidermis; palisade several rows of shorter cells or two rows of longer; all mesophyll cells elongated perpendicularly to the surface; stomata sunken one-half the depth of the epidermal cells. Stem with xylem cylinder very woody; walls of pith and medullary ray cells heavy; cortex and phloem zones very narrow; cork layer not strikingly thick but very dense; 9 years' growth in a stem 4 mm. in diameter.

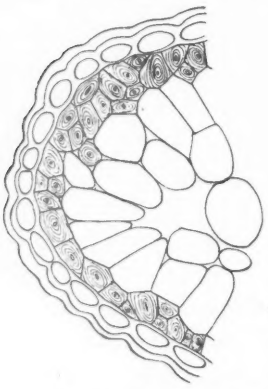


FIG. 2.—*Juniperus communis:* section of leaf.

Juniperus communis (fig. 2).—An erect evergreen shrub. Leaf thick, rigid, convex on one side, concave on the other which is the morphological upper side and is most protected when the leaves are appressed to the stem; stomata on this side at the base of the epidermal cells, guard cells with thickened walls; outer and side walls of epidermis thick, outer 11–13 μ with cuticle 3.2 μ; hypodermis heavy; resin duct on convex side. Stem with almost no pith and heavy wood cylinder; 13 years' stem 4 mm. in diameter; cork thick.

Juniperus virginiana.—A shrub or small tree. Leaf awl-shaped; outer wall of epidermis very heavy, 9.6 μ, cuticle 4.8 μ; two or three hypodermal layers on the convex side of the leaf heavily thickened; sunken stomata on upper plane surface, the protected side when the leaf is appressed. Stem with solid mass of heavy-walled tracheids and almost no pith; 11 growth rings in a stem 4.5 mm. in diameter; rows of sclereids in the cortex; cork thick.

Hypericum Kalmianum (fig. 3).—A bushy shrub. Leaf revolute, thick, leathery; outer wall of epidermis 4.8 μ, cuticle 2.4 μ, lower epidermal cells inclined to be papillate; double palisade; stomata sunken the depth of the epidermis. Stem with vessels large, fibers heavy, lumen small; pith small, cork thick; three growth rings in a stem 3 mm. in diameter.

Trees

Pinus Banksiana.—Leaf shorter and thicker than in most pines; walls of epidermis heavy; outer 8 μ, cuticle 1.8 μ; hypodermis also heavy; thickness of both increased at the edges of the leaf; outer wall of endodermis thickened and lignified; mesophyll cells with infoldings in the walls; stomata deeply sunken, with an outer and inner vestibule and with walls 3.2 μ thick; two resin ducts. Stem with small pith; woody cylinder large, composed of a solid mass of tracheids with very thick walls.

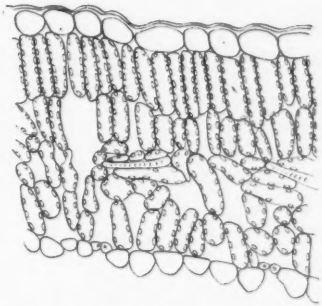


FIG. 3.—*Hypericum Kalmianum*: section of leaf.

Quercus velutina.—Small in comparison with many oaks, and of rather scrubby growth. Leaf thick, having a brilliantly varnished surface; sclerenchyma around the bundles of the midrib; cells above and below collenchymatous; epidermal cells over midrib papillate; outer wall of upper and lower epidermis thickened, cuticle thick; palisade double. Stem with pith star-shaped; vessels large; fibers heavy, with small lumen; medullary rays narrow, pith sclerenchymatous; an irregular band of fibers in the cortex.

Summary of xerophytic characters

The true dune plants have the following characteristics, which, with the exception of the characters of the conductive system, are generally admitted to be xerophytic:

HABIT.—Low, tufted, or bushy, with short internodes (*Arenaria, Artemisia, Hudsonia, Juniperus communis, J. virginiana*); low

and spreading (*Prunus pumila, Salix syrticola*); low and trailing (*Lathyrus, Arctostaphylos*); low, with underground, creeping rootstocks (*Ammophila, Calamovilfa*).

LEAF.—Small and awl-shaped (*Arenaria, Hudsonia, Juniperus communis, J. virginiana*); longer, sometimes wide but thick (*Artemisia, Ammophila, Calamovilfa, Lithospermum, Prunus, Arctostaphylos, Pinus, Hypericum, Cakile, Quercus, Corispermum*); evergreen (*Arctostaphylos, Juniperus communis, J. virginiana, Pinus*); folded or revolute (*Cirsium, Ammophila, Calamovilfa, Lithospermum, Hypericum, Euphorbia polygonifolia*); succulent (*Cakile, Euphorbia polygonifolia, Corispermum*, slight in *Artemisia, Cirsium, Solidago*); hairy (*Artemisia, Cirsium, Lithospermum, Salix syrticola, Hudsonia*); equilateral (*Cakile, Corispermum, Artemisia, Cirsium, Lithospermum*).

ANATOMY OF LEAF.—Outer wall of epidermis thick (*Cakile, Euphorbia polygonifolia, Corispermum, Artemisia, Cirsium, Ammophila, Calamovilfa, Andropogon, Solidago, Lithospermum, Arenaria, Prunus pumila, Salix syrticola, Arctostaphylos, Juniperus communis, J. virginiana, Pinus Banksiana, Hypericum, Quercus velutina, Opuntia*); cuticle thick (*Ammophila, Calamovilfa, Andropogon, Solidago, Arenaria, Prunus pumila, Arctostaphylos, Juniperus communis, J. virginiana, Pinus Banksiana, Hypericum, Quercus, Opuntia*); deep, compact palisade accompanied by few air spaces in sponge (*Artemisia, Lathyrus, Lithospermum, Prunus pumila, Salix syrticola, Hudsonia, Arctostaphylos, Hypericum, Quercus velutina, Cakile, Corispermum*); stomata sunken (*Artemisia, Ammophila, Calamovilfa, Hypericum, Euphorbia polygonifolia, Arctostaphylos, Juniperus communis, J. virginiana, Pinus*); conductive tissue well developed (*Solidago, Prunus, Arctostaphylos*); mechanical tissue present as sclerenchyma (*Lathyrus, Ammophila, Calamovilfa, Andropogon, Salix syrticola, Arctostaphylos, Quercus*), as collenchyma (*Solidago, Andropogon, Prunus, Salix syrticola, Arctostaphylos, Quercus, Euphorbia polygonifolia*).

ANATOMY OF STEM.—Succulent (*Opuntia*); conductive tissue well developed, with vessels large (*Cirsium, Lithospermum, Prunus, Hypericum, Quercus*), with vessels numerous (*Salix syrticola, Prunus pumila*); mechanical tissue present, an abundance of wood

fibers giving general "woodiness" (*Euphorbia polygonifolia, Artemisia, Cirsium, Lithospermum, Prunus, Salix syrticola, Hudsonia, Arctostaphylos, Pinus, Hypericum, Juniperus communis, J. virginiana, Quercus*), as sclerenchyma (*Artemisia, Lathyrus, Ammophila, Solidago, Prunus pumila, Salix syrticola, Hudsonia, Quercus, Juniperus virginiana*), as collenchyma (*Artemisia, Cirsium, Solidago, Lithospermum, Salix syrticola, Pinus, Corispermum*); outer wall of epidermis thick (*Cakile, Euphorbia, Lathyrus, Ammophila, Lithospermum*); cork thick (*Artemisia, Prunus, Hypericum, Juniperus communis, J. virginiana*).

ANATOMY OF ROOT.—Sclerenchymatous generally (*Cakile, Corispermum, Lathyrus, Solidago*); collenchyma in cortex (*Solidago*); crystals abundant (*Solidago, Arenaria, Prunus*); resin (*Juniperus communis, J. virginiana, Pinus*); latex (*Euphorbia*); perhaps none but the last is related to xerophytic conditions.

Slowness of growth is shown by the large number of growth rings in stems of small size (*Arctostaphylos, Hypericum, Juniperus communis, J. virginiana*), testifying to adverse conditions. Succulency usually excludes some other factors, as hairiness and good development of conductive elements.

FITTING (**11**) has recently shown that desert plants apparently do not need longer roots to reach an abundant water supply, as they have a most effective means of obtaining it from a very scanty supply in the high osmotic pressure of their cell sap. Dune plants have not been examined in this respect. It may be found that they too have this "adaptation" to xerophytic conditions.

II. COMPARISON OF PLANTS GROWING ON THE DUNES WITH THE SAME SPECIES GROWING IN MESOPHYTIC SITUATIONS

The purpose of this part of the investigation was to find out by careful measurements just how much variation there is in species found in two widely differing habitats. The measurements of sections were made with a micrometer divided into 100 spaces. For the measurement of the leaf, sections were made near the middle, cutting straight across the midrib; an average was taken of several measurements of one leaf and then of several leaves. For

the study of the conducting and mechanical tissues of the leaf, a section of the midrib was taken at the base of the blade. For the study of the stems, sections 5 mm. in diameter were used; when this was not possible, the two compared were as nearly equal as obtainable. CANNON'S method of counting was adopted. A circle 14 cm. in diameter was drawn on paper and octants were marked off. With a camera lucida an image of the section was so thrown on the paper that the arc of the octant coincided as nearly as possible with the periphery of the wood cylinder. The area of the octant was 18.24 sq. cm. ($14^2 \times 0.7845 \div 8$). Since the magnification used was 100, the area examined was 0.19 sq. cm. or 19 sq. mm. For the size of the vessels and fibers measurements were always made in the last spring wood, or if that was not fully organized, in the preceding. In the following tables *M* stands for the mesophytic form and *X* for the dune form; *T* for the average thickness of leaf, with minimum and maximum in parenthesis; *UE* for thickness of the upper epidermis, including cuticle; *P* for depth of palisade; *Sp* for depth of sponge; *LE* for thickness of lower epidermis; *OW* for outer wall of the epidermis (including cuticle); and *Cu* for cuticle. The percentages are of the entire thickness of the leaf. In the table of stems *N* stands for the number of vessels in the octant; *D* for the average diameter of the larger vessels, with the maximum in parenthesis; *W*, the thickness of the walls of the vessels; *F*, the thickness of the walls of the fibers; *L*, the lumen of the fibers; *R*, the number of growth rings; *C*, the thickness of cork; and *S*, the thickness of the sclerenchyma ring or of the isolated masses of sclerenchyma that often appear in the cortex. As the size of vessels, being tubes, varies as their cross-sections and as the cross-sections vary as the squares of their radii, it is evident that the vessels in an octant of a mesophytic form would compare with the vessels in an octant of the corresponding dune form as the products of the number of vessels by the squares of their radii. Where the result is not evident at a glance, the radius was squared and the product found. The measurements are all in microns, though the μ is omitted after the first, as is also the per cent sign.

Trees

ACER SACCHARUM

Leaf			Stem		
	M	*X*		*M*	*X*
T.....	75 μ (69–93)	103 μ (95–109)	N...	41	33
UE...	10.5 = 14 per cent	13 = 12 per cent	D...	36 μ (50)	37 μ (46)
P.....	29.5 = 39	40 = 39	W...	3	3.5
Sp....	29.0 = 39	40 = 39	F....	4.2	4.7
LE...	6.0 = 8	10 = 10	L....	6.2	8.5
OW...	1.6	3.5	R...	3–5	2–4
Cu...	thin	1.7	C....	80	72
			S....	64	50

X.—Hairs on lower surface; upper epidermal cells smaller in depth, slightly larger in surface extent; outer wall and cuticle thicker; sclerenchyma around the bundles of the midrib heavier; greater development of bundles; cuticle on upper surface more strongly ridged. In both stomata on lower surface only.

In all points but the thickness of the walls of the vessels and the fibers, an exception to the majority of cases examined.

CELTIS OCCIDENTALIS

Leaf			Stem		
	M	*X*		*M*	*X*
T.....	65 μ (87–72)	120 μ (104–144)	N...	17	18.5
UE...	13 = 20 per cent	24 = 20 per cent	D...	74 μ (101)	74 μ (120)
P.....	14 = 22	43 = 36	W...	2.4	3.2
Sp....	24 = 37	40 = 33	F....	4.8	6.4
LE...	14 = 21	13 = 11	L....	4.8	3.2
OW...	0.7	3	R...	7	7
Cu...	very thin	0.7	C....	48	32
			S....	64	80

X.—Large glandular cells frequently occupying the place of the epidermis and palisade; collenchyma below and sclerenchyma above the midrib, where neither appears in the mesophytic form; greater development of vascular elements.—Figs. 4 and 5.

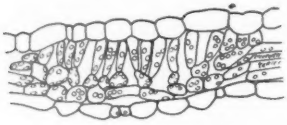
X.—A straggling shrub, probably var. *pumila;* slightly greater development of vessels with heavier walls; fibers heavier, but fewer of them than in *M*, replaced by tracheids; cork thinner; more sclerenchyma in the cortex.

FRAXINUS AMERICANA

Leaf		Stem	
M	*X*	*M*	*X*
T.....142 μ (124–159)	162 μ (142–187)	N... 22.5	19.5
UE... 11 = 8 per cent	14 = 9 per cent	D... 53 μ (87)	51 μ (72)
P..... 52 =36	68 =42	W... 3.7	3.9
Sp.... 68 =48	59 =36	F.... 3.2	4.5
LE... 11 = 8	21 =13	L.... 7.2	7.3
OW... 1.5	3	R... 88	110
Cu... 0.7	1.8	C.... 53	99
		S.... 3–5	1–2

X.—Epidermal cells of greater depth; outer wall and cuticle thicker, ridged in the lower epidermis, most of the cells of the lower epidermis produced into short conical hairs, the rest into long hairs (*M* smooth); all tissue more compact; palisade deeper, tending to develop four rows (*M* only two); vessels in the midrib more numerous but not larger; walls thicker; greater development of fibers about the stele. Both have conspicuous glands on the upper surface, and stomata on lower surface only.—Figs. 6 and 7.

X.—Differing from the majority in number and size of vessels and more rapid growth; walls of vessels and fibers thicker; sclerenchyma and cork heavier. In both walls of pith-cells thickened with conspicuous canals, and outer cortex collenchymatous, features pronounced in *X*.



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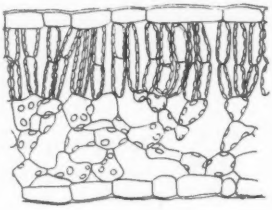

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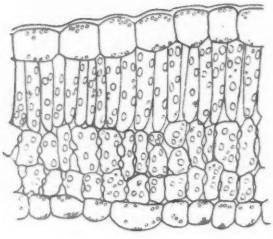

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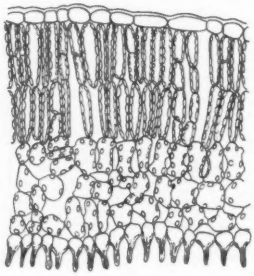

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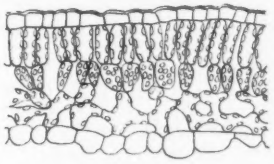
FIGS. 4–7.—Figs. 4 and 5, *Celtis occidentalis:* sections of leaves; fig. 4, mesophytic form; fig. 5, dune form; figs. 6 and 7, *Fraxinus americana:* sections of leaves; fig. 6, mesophytic form; fig. 7, dune form.

JUGLANS CINEREA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.....	92 μ (79–112)	148 μ (119–166)	N... 18	25
UE...	12 =13 per cent	13 = 9 per cent	D... 64 μ (85)	55 μ (79)
P.....	21 =21	39 =26	W... 7.3	3.8
Sp....	44 =48	82 =55	F.... 4	3.2
LE...	14 =16	14 =10	L.... 9.5	9
OW...	thin	3.7	R... 1–6 (av. 3)	1–3
			C.... 60	57
			S.... 73	77

X.—More pubescent; upper epidermal cells smaller in depth, same in surface extent; first layer of palisade deeper and a second layer developed; vessels in midrib of the same size but more numerous; more sclerenchyma and collenchyma; crystals abundant.—Figs. 8 and 9.

X.—Like the majority in the greater number of vessels of smaller area (but the final product greater), the smaller lumen of the fibers, and the heavier sclerenchyma; differing in thinner walls and cork, and occasionally large number of rings produced in *M*



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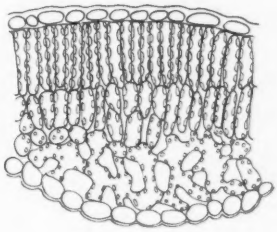

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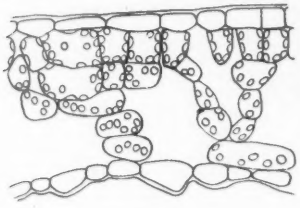
FIGS. 8, 9.—*Juglans cinerea:* sections of leaves; fig. 8, mesophytic form; fig. 9, dune form.

LIRIODENDRON

Leaf			Stem		
	M	*X*		*M*	*X*
T.	148 μ (137–168)	210 μ (190–236)	N.	79	131
UE.	15 = 10 per cent	17 = 8 per cent	D.	34 μ (48)	32 μ (41)
P.	37 = 25	59 = 28	W.	3.1	3.2
Sp.	80 = 54	111 = 53	F.	3.8	4.6
LE.	16 = 11	22 = 11	L.	10.7	8.5
OW.	3.3	5.6	R.	1–3	2–5
Cu		2	C.	42	50
			S		

X.—Cells of upper epidermis smaller in surface and depth, side walls plane (wavy in *M*); palisade deeper, sometimes of more layers; cells of upper layer each side of midrib larger than others and without chloroplasts, as if a secondary epidermis; vessels more numerous in midrib; greater masses of fibers and more collenchyma. In both, lower epidermis heavy.—Figs. 10 and 11.



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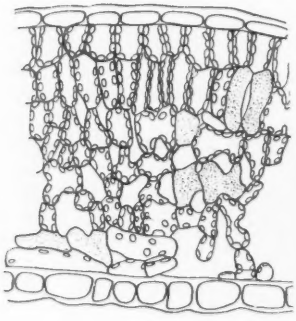

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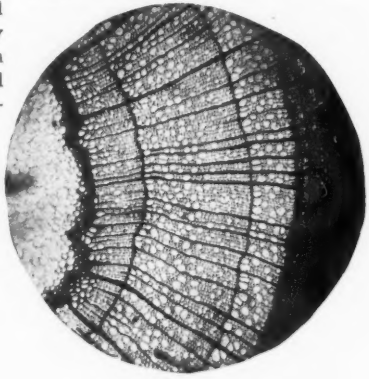
Like the majority in all respects. In both, sclerenchyma around the pith and groups of fibers capping the phloem.—Figs. 12 and 13.



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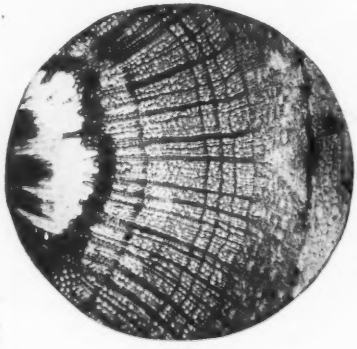


13

FIGS. 10–13.—*Liriodendron tulipifera:* sections of leaves; fig. 10, mesophytic form; fig. 11, dune form; sections of stems; fig. 12, mesophytic form; fig. 13, dune form.

OSTRYA VIRGINIANA

Leaf			Stem		
	M	*X*		*M*	*X*
T.....	78 μ (66–95)	110 μ (91–125)	N...	24	59
UE...	10 = 11 per cent	11 = 10 per cent	D...	48 μ (75)	26 μ (37)
P.....	30 = 38	43 = 39	W...	2.8	2.5
Sp....	32	45	F....	3.3	3.9
LE...	6	11	L....	6.7	5.6
OW...	1.3	3.2	R...	3	3–6
			C....	29	64

X.—Upper epidermis slightly thicker and wall thicker; little variation in the depth of the palisade, but the layer more compact; stomata on lower surface only (in *M* occasionally on the upper).

X.—Rings of sclerenchyma in the cortex wider and outer layers of the pith more sclerenchymatous; in all respects, except as to the thickness of the wall of the vessels, agreeing with the majority.

POPULUS BALSAMIFERA

Leaf			Stem		
	M.	*X*		*M*	*X*
T.....257 μ (243–272)		212 μ (195–228)	N 33		90
UE... 18 = 7 per cent		17 = 8 per cent	D...	46 μ (62)	36 μ (50)
P..... 96 = 37		94 = 44	W...	2.9	2.6
Sp....129		89	F....	4.1	3.8
LE... 14		16	L....	7.2	6.8
OW... 4.3		5	R...	1–2	2–9
Cu... 1		1.2	C....		100
			S....	64	90

The only exception found to the general fact that dune plants have thicker leaves than mesophytic. *X*.—Upper epidermis and palisade relatively deeper; outer wall and cuticle thicker and ridged; more vessels in the midrib, larger; more fibers about the stele. Both have stomata on both surfaces; all side walls of epidermis plane except those of lower surface in *M;* double palisade.

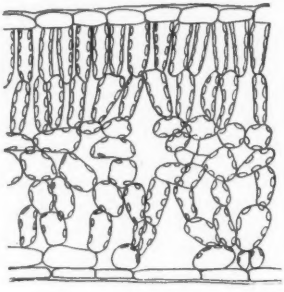
X.—Vessels agreeing with the majority in total area, but walls slightly thinner, walls of fibers also thinner, but lumen smaller, so the amount of wood may be the same; cork only starting to form in *M*.

POPULUS DELTOIDES

	Leaf		Stem	
	M	*X*	*M*	*X*
T.	193 μ (177–227)	254 μ (236–295)		
UE.	13 = 7 per cent	18 = 7 per cent		
P.	62 = 32	84 = 33		
Sp.	105 = 54	138 = 55		
LE.	13	14 = 5		
OW.	2.3	4		
Cu.	0.8	1.3		
N.			46	85
D.			49 μ (64)	50 μ (62)
W.			2.6	2.7
F.			3.8	3.9
L.			6.8	6
R.			2	1–4
C.			82	105
S.			94	98

In both lower epidermis thickened as well as upper, stomata on both surfaces and side walls of epidermal cells plane, all related to the movement of the leaf. *X*.—Upper epidermal cells smaller in surface; surface slightly hairy; palisade sometimes triple; also palisade cells near lower epidermis, separated from it by a layer of heavily walled cells, like a secondary epidermis. Other points follow the general rule.—Figs. 14 and 15.

Agreeing with the majority in all points; a tendency to angled twigs and star-shaped pith more marked in *X*.



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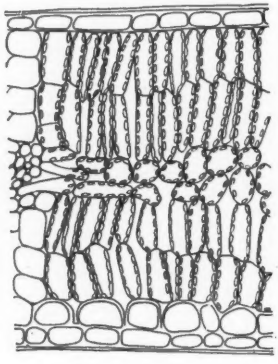


15

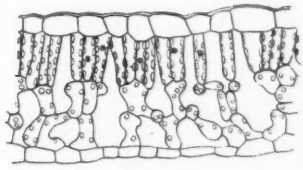
FIGS. 14, 15.—*Populus deltoides:* sections of leaves; fig. 14, mesophytic form; fig. 15, dune form.

TILIA AMERICANA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.....	90 μ (90–108)	138 μ (135–156)	N... 59	63
UE...	17 =19 per cent	23 =17 per cent	D... 38 μ (53)	41 μ (41)
P.....	26 =29	45 =33	W... 2.7	2.8
Sp....	36 =46	52 =38	F.... 2.8	2.4
LE...	11 =12	17 =12	L.... 9.6	9.1
OW...	3.7	4.4	R.... 2–5	1–5
Cu...	1.5	2	C.... 58	50

X.—Cells of upper epidermis smaller in depth, larger in surface, sometimes divided periclinally; side walls on lower surface wavy, upper and both in *M* plane; deeper palisade and tendency toward second layer; midrib as in preceding *X*. In both hairs in the axils of the veins; cuticle ridged.—Figs. 16 and 17.

In both bands of sclerenchyma in the phloem and collenchyma under the cork, slightly less in *X;* little variation in walls and lumina of the fibers, but vessels more numerous and larger in *X*.



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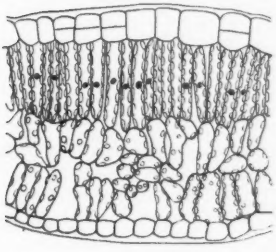


17

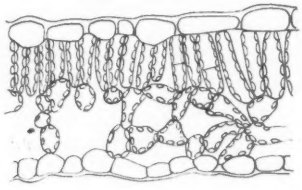
FIGS. 16 and 17.—*Tilia americana:* sections of leaves; fig. 16, mesophytic form; fig. 17, dune form.

ULMUS AMERICANA

Leaf			Stem		
	M	*X*		*M*	*X*
T.....102 μ (94–109)		174 μ (164–186)	N... 28.5		52
UE... 21 =21 per cent		38 =22 per cent	D... 61 μ (104)		61 μ (96)
P..... 29 =29		70 =40	W... 3.7		3.3
Sp.... 38 =37		51 =29	F.... 5.9		5.7
LE... 13 =13		15 =9	L.... 2.9		3.7
OW... 3.2		5.2	R... 5–11		5
Cu...thin		thin	C.... 66		66

X.—Cells of upper epidermis greater in depth; side walls plane, cuticle not ridged (in *M* walls slightly wavy and cuticle slightly ridged on lower surface); palisade deeper sometimes double, midrib structure as in other *X*. In both upper surface rough, hairy (*X* more so); some epidermal cells enormous.—Figs. 18 and 19.

Vessels as in majority. *X*.—Walls of vessels and of fibers very slightly thinner than in *M* and lumina of fibers larger, yet masses of fibers so much more numerous they form more wood; cork and cortical sclerenchyma the same.



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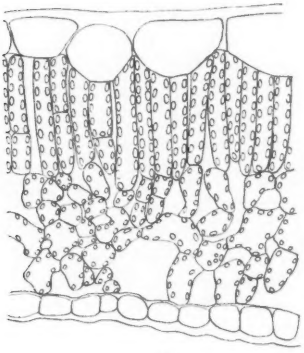


19

FIGS. 18 and 19.—*Ulmus americana:* sections of leaves; fig. 18, mesophytic form; fig. 19, dune form.

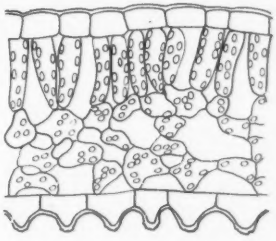
Shrubs

CORNUS STOLONIFERA

Leaf				Stem			
	M		*X*		*M*		*X*
T.	129 μ (120–144)		156 μ	N.	63		70
UE.	17	=13 per cent	15 =10 per cent	D.	30 μ (41)		33 μ (45)
P.	34	=26	48 =31	W.	3.2		34
Sp.	56	=44	72 =46	F.	4.7		5
LE.	22	=17	21 =13	L.	6.4		6.2
OW.	1.6		2	R.	1–3		2–8
Cu.	thin		0.8	C.	None except at lenticels		112 (in 8-year stem)

X.—Hairs more abundant than in *M*, on upper surface radiating from a center parallel to the surface, tuberculate; on lower surface simple or branched; short hairs also found, formed as slight prolongations of most of the lower epidermal cells, their cuticle prominently ridged; cells of upper epidermis smaller in all dimensions; side walls plane (wavy in *M*); deposits in the form of crystals and oil in the cells, and wax on the outer wall; other points as in most xerophytic forms.—Figs. 20 and 21.

Epidermal cells when present papillate and cuticle heavy; cork not formed before 5 years. In both small groups of sclerenchyma in cortex. All points as in majority.



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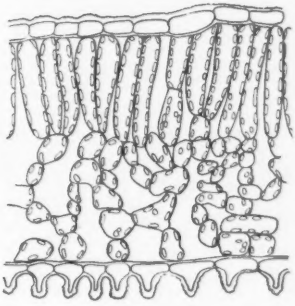


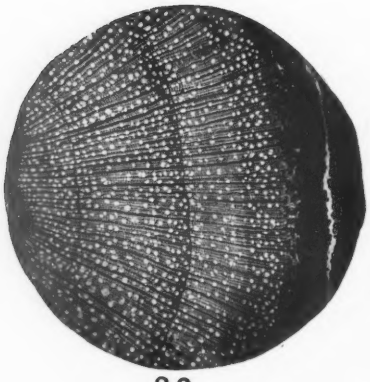
21

FIGS. 20, 21.—*Cornus stolonifera:* sections of leaves; fig. 20, mesophytic form; fig. 21, dune form.

HAMAMELIS VIRGINIANA

Stem (figs. 22 and 23)

	M	*X*
N...	94	157
D...	29 μ (37)	24 μ (27)
W...	2.3	1.6
F....	5.7	6.4
L....	5.6	4
R...	3	5
C....	56	48
S....	64	88



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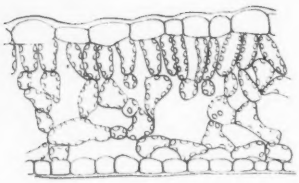

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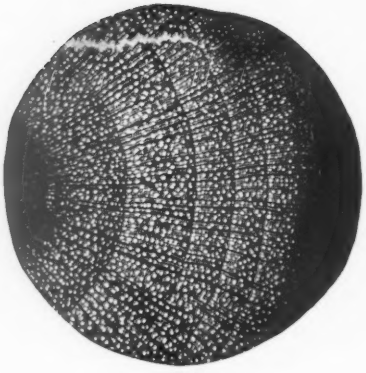

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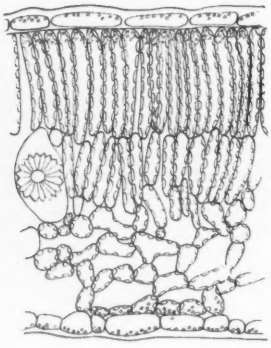


25

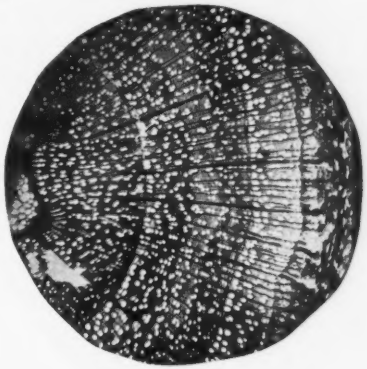
FIGS. 22–25.—Figs. 22 and 23, *Hamamelis virginiana:* sections of stems; fig. 22, mesophytic form; fig. 23, dune form; figs. 24 and 25.—*Prunus virginiana:* sections of leaves; fig. 24, mesophytic form; fig. 25, dune form.

PRUNUS VIRGINIANA

	Leaf		Stem	
	M	*X*	*M*	*X*
T.	119 μ (100–123)	198 μ (187–214)	N. 76	108
UE.	18 = 15 per cent	16 = 8 per cent	D. 38 μ (55)	35 μ (45)
P.	35 = 30	99 = 50	W. 3.1	3.5
Sp.	51 = 43	66 = 33	F. 4.6	4.6
LE.	14 = 12	17 = 9	L. 4.7	4.4
OW.	2.9	6.7	R. 3	3–6
Cu.	1.1	1.8	C. 42	61
			S. 83	51

X.—Hairs on lower surface (none in *M*); cells of upper epidermis larger in surface, of less depth, cuticle more prominently ridged than in *M;* side walls less wavy; palisade double (sometimes so in *M*, but cells are not so long nor so compact as in *X*); midrib as in other *X* (sometimes in *M* sclerenchyma below the stele is scarcely perceptible); oil drops, especially in epidermis and upper part of palisade; crystals and other deposits about the bundles.—Figs. 24 and 25.

Only exception to the majority rule is the sclerenchyma, which is heavier in some mesophytic forms.—Figs. 26 and 27.



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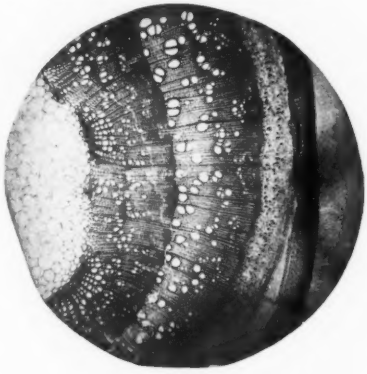
FIGS. 26–27.—*Prunus virginiana:* sections of stems; fig. 26, mesophytic form; fig. 27, dune form.

PTELEA TRIFOLIATA

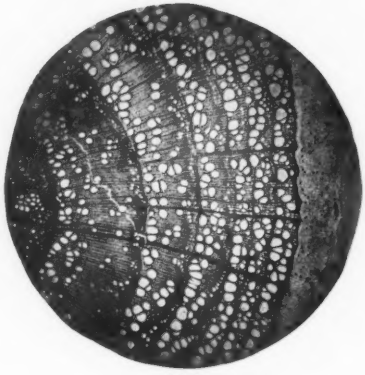
	Leaf		Stem	
	M	*X*	*M*	*X*
T	147 μ (131–156)	185 μ (177–193)	N ... 51	51
UE	14 = 9 per cent	18 = 10 per cent	D ... 53 μ (73)	55 μ (82)
P	42 = 29	56 = 30	W ... 2.2	3.1
Sp	78 = 53	95 = 51	F 2	2.9
LE	13 = 9	16 = 9	L 8.4	7.2
OW	1.2	4.8	R ... 2–3	4–7
Cu	thin	1.3	C ... 50	83

X.—Hairs abundant on lower surface (none in *M*); cells of upper epidermis slightly larger in surface; side walls on both surfaces plane and cuticle ridged (in *M* wavy and only slightly ridged); palisade, sponge, and midrib as in other *X*. One tree in an especially exposed situation, near the top of a wind sweep leading up from the lake, probably once a mesophytic pocket, had a more pronounced structure than the one figured; the leaf averaged 210 μ in thickness, with an outer wall 6.4–8 μ, heavily cutinized.

Agreeing with the majority, except that collenchyma in outer cortex may be no heavier in *X*.—Figs. 28 and 29.



28



29

FIGS. 28–29.—*Ptelea trifoliata:* sections of stems; fig. 28, mesophytic form; fig. 29, dune form.

SALIX LONGIFOLIA

Leaf		Stem	
M	*X*	*M*	*X*
T.....152 μ (136–168)	188 μ (162–212)	N... 77	66.5
UE... 8 = 5 per cent	12 = 6 per cent	D... 36 μ (53)	43 μ (55.5)
Mes..133 =88	165 =88	W... 2.4	2.4
LE... 11 = 7	11 = 6	F.... 2.8	3
OW... 1.5	3	L.... 5.3	6.7
Cu...thin	2	R... 4	2
		C.... 33	32
		S.... 33	48

Equilateral; two rows of palisade on each side beneath a hypodermis, differentiated as a special storage region; stomata on both surfaces, slightly sunken. *X*.—Upper palisade cells more elongated; sclerenchyma and collenchyma more abundant in midrib.

X.—Agreeing with the majority in the greater area of vessels and greater number and size of sclerenchyma masses in the cortex; exceptional in the larger lumen of the fibers and fewer growth rings.

Lianas

CELASTRUS SCANDENS

Leaf		Stem	
M	*X*	*M*	*X*
T.....101 μ (92–123)	164 μ (138–174)	N... 36	37
UE... 14 =14 per cent	22 =14 per cent	D... 54 μ (78)	45.5 μ (69)
P..... 25 =25	43 =26	W... 2.8	3.6
Sp.... 49 =48	81 =49	F.... 4.9	4.5
LE... 13 =13	18= 11	L.... 8.4	7.5
OW } thin	4	R... 1–3	1–3
Cu }	1.7	C.... 80	76

X.—Coarse, often merely acute; veins prominent on the under side. *M*.—Smooth and fine, long acuminate; veins not prominent on under side; other variations as usual.

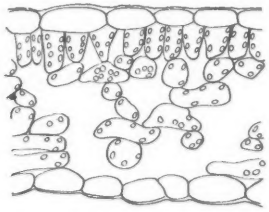
Chiefly an exception; *M* greater in area of vessels, heavier fibers and cork. *X* follows the majority in having heavier sclerenchyma around the pith, thicker walls of the vessels, and smaller lumina in the fibers.

PSEDERA QUINQUEFOLIA

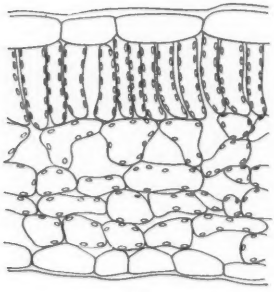
	Leaf		Stem	
	M	*X*	*M*	*X*
T.	110 μ (99–130)	183 μ (164–195)		
UE.	14 = 13 per cent	21 = 11 per cent		
P.	24 = 22	56 = 31		
Sp.	59 = 53	90 = 49		
LE.	13 = 12	16 = 9		
OW.	1.5	3		
Cu.	0.7	1.5		
N.			36	40.5
D.			78 μ (120)	61 μ (90)
W.			2.8	3.4
F.			4.6	5.9
L.			7.2	4.7
R.			1	1.2
C.			196	188
S.			112	62

In both side walls of epidermal cells plane except in lower surface of *M*, cuticle ridged, hairs on the lower surface. *X*.—Epidermal cells larger in surface, smaller in depth; other points as usual except there is not greater development of conductive tissues.—Figs. 30 and 31.

Exceptional in the smaller area of cross-sections of vessels in *X*, less sclerenchyma and cork; the cork is loose and shreds off, so more may have been lost in *X* than in *M;* the other points agree with the majority.



30



31

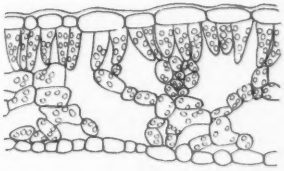
FIGS. 30, 31.—*Psedera quinquefolia:* sections of leaves; fig. 30, mesophytic form; fig. 31, dune form.

RHUS TOXICODENDRON

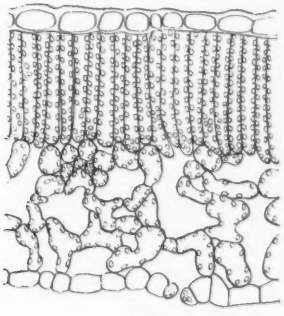
Leaf			Stem		
	M	*X*		*M*	*X*
T.....	79 μ (73–116)	140 μ (123–198)	N...	35.5	18.5
UE...	9 =11 per cent	12 = 9 per cent	D...	85 μ (99)	69 μ (88)
P.....	25 =33	45 =32	W...	2	2.4
Sp....	37 =46	70 =56	F....	2.4	2.8
LE...	8 =10	12 = 9	L....	9.6	7.2
OW...	1.9	2.7	R...	2	3
Cu...thin		1.4	C....183		145

X.—Epidermal cells smaller in depth; occasional indications of a double palisade; other points as usual.—Figs. 32 and 33.

Exceptional but in the mass of wood formed.



32



33

FIGS. 32–33.—*Rhus toxicodendron:* sections of leaves; fig. 32, mesophytic form; fig. 33, dune form.

SMILAX HISPIDA

Leaf

	M	*X*
T.	106 μ (96–129)	168 μ (157–204)
UE.	11 = 11 per cent	22 = 13 per cent
Mes.	82 = 77	124 = 74
LE.	13 = 12	22 = 13
OW.	1.5	3.7
Cu.	thin	1

X.—Epidermal cells deeper and larger in surface extent; outer wall and cuticle heavier; cuticle more strongly ridged; side walls less wavy; more conductive and mechanical tissues, but walls thinner. The mesophyll shows the usual monocot variation, no differentiation into palisade and sponge.

Stem

(Quadrant used instead of octant)

	M	*X*
N.	6 bundles; each with 2 large vessels and 18 smaller	6 2 13
D.	of large vessels 105	107
W.	4	4
F.	3.2	3.6
L.	5.9	4.3
OW.	18	22

X.—Two vessels larger, but not so many small ones; cortex more collenchymatous; pith cells with thicker walls, pith packed with starch grains and crystals.

VITIS VULPINA

Leaf

	M	*X*
T.	105 μ (100–118)	153 μ (127–164)
UE.	14 = 13 per cent	13 = 9 per cent
P.	28	45 = 29
S.	50	81 = 53
LE.	13	14 = 9+
OW	thin	1.8
Cu	thin	1

X.—Upper epidermal cells smaller in depth, larger in surface; hairs on veins on both surfaces (only on upper in *M*); other points as usual. In both walls plane and cuticle somewhat ridged.

Stem

	M	*X*
N.	9	10
D.	105 μ (142)	102 μ (127)
W.	4	4.5
F.	5.2	4.8
L.	7.2	7.1
R.	2–3	2–3
C.	236	307

X.—Slightly more area in cross-sections of vessels; cork thicker; less sclerenchyma.

Herbs

ASCLEPIAS SYRIACA

Leaf

	M	*X*
T.	225 μ (230–296)	272 μ (237–304)
UE.	25 = 10 per cent	25 = 9 per cent
P.	54 = 21	77 = 28
Sp.	158 = 62	151 = 56
LE.	18 = 7	19 = 7
OW.	2.4	2.4

Stem

	M	*X*
N.	25	18
D.	46 μ (66)	64 μ (87)
W.	3.5	4.6
F.	2.9	3.5
L.	17	15
OW.	4	6.4
Wood cyl	185	611

In both side walls of upper epidermal cells plane, of lower wavy; cuticle ridged on lower surface. *X*.—Hairs on both surfaces (only on lower in *M*); upper epidermal cells smaller in depth, larger in surface; palisades often deep in proportion to sponge; where not, a secondary palisade partly organized; conductive and supporting tissues as usual; latex and other secretions more abundant.—Figs. 34 and 35.

X.—Area of cross-sections of vessels smaller, larger cylinder of wood formed; walls of vessels and of fibers heavier, lumen of fibers smaller, so more wood; outer wall of epidermis and hypodermal collenchyma heavier.

SMILACINA STELLATA

Leaf

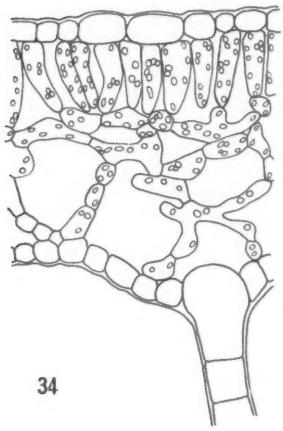
	M	*X*
T.	174 μ (155–199)	202 μ (182–242)
UE.	28 = 16 per cent	30 = 15 per cent
M.	119 = 68	144 = 71
LE.	27 = 16	29 = 14
OW.	2.6	2.9
Cu.	0.7	0.7

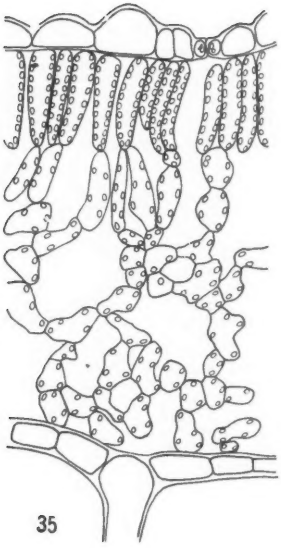
Stem

	M	*X*
Bundles in field	12	12
N in bundle	15	13
D.	27 μ	32 μ
W.	4.3	4.5
OW.	7.2	6.4

X.—Epidermal cells smaller in depth, larger in surface; hairs more abundant, more crystals deposited; other variations as usual; in both no differentiation in the mesophyll, the general monocot situation; side walls of epidermal cells plane.

X.—Area of cross-sections of vessels greater; walls of vessels heavier, but outer wall thinner.





FIGS. 34, 35.—*Asclepias syriaca:* sections of leaves; fig. 34, mesophytic form; fig. 35, dune form.

Swamp forms

Sometimes a moving dune passes over a swamp association, and the members by increased length of stem keep pace with it for a time; a few of these have been examined and compared with forms growing in their natural habitat.

PLATANUS OCCIDENTALIS

	Leaf		Stem	
	S	*X*	*S*	*X*
T.	152 μ (136–162)	199 μ (162–205)		
UE.	23 = 15 per cent	25 = 12 per cent		
P.	52 = 34	63 = 32		
Sp.	62 = 41	92 = 46		
LE.	16 = 10	19 = 10		
OW.	4	2.8		
N.			66	69
D.			35 μ (50)	46 μ (63)
W.			3.2	3.2
F.			5	3.2
L.			6.4	7
R.			3	2
C.			68	6.9
S.			100	116
Collen			56	109

The dune form has thicker leaves than the swamp form, but the palisade and outer wall of the epidermis are exceptional.

The dune form shows an increase in number and size of the vessels, but there is no increase in woody tissue furnished by the fibers. There seems to be no diminution in growth as indicated by the growth rings, but mechanical tissue outside the stele and the cork have increased.

ALNUS INCANA

	Stem	
	S	*X*
N.	68	61
D.	29	34
W.	2.5	2.6
F.	3.5	3.4
L.	7	8.8

Swamp form, vessels larger than the others but fewer in number. Dune form, larger area of vessels. Thickness of walls about the same.

CEPHALANTHUS OCCIDENTALIS

	Leaf	
	S	*X*
T.	175 μ (143–168)	163 μ (147–189)
UE	16 = 9 per cent	17 = 10 per cent
P.	54 = 31	48 = 29
Sp.	91 = 52	84 = 52
LE.	14 = 8	14 = 9
OW	3	3.7
Cu.	1.6	2

A second layer of palisade is partly organized in the swamp form and completely in the dune form. The first palisade is relatively shorter in the dune form, but the second is so much more compact than in the swamp form that it must more than make up the amount of tissue. In both forms stomata are found on the lower surface only and the side walls of the epidermal cells are waxy.

SALIX GLAUCOPHYLLA

	Leaf		Stem	
	M	*X*	*S*	*X*
T.	185 μ (180–208)	231 μ (219–240)	N. 57	64
UE.	20 = 10 per cent	19 = 9 per cent	D. 45	47
P.	92 = 50	120 = 52	W. 2.3	2.4
Sp.	57 = 31	69 = 30	F. 3.1	4.8
LE.	16 = 8	19 = 9	L. 5	3.2
OW.	4.3	4.8	R. 2–4	4
Cu.	1.6	1.6	Cork. 56	80
			Collen 4–6 layers	7 layers

Little variation, but the palisade is slightly deeper in the dune form; the vessels of the midrib are larger though about as numerous, their walls are heavier as is also the outer epidermal wall, and there is more collenchyma.

In the dune form more vessels and larger; the fibers heavier and the lumina smaller, giving more wood; growth rings about the same; more cork, collenchyma, and sclerenchyma.

CORNUS STOLONIFERA

A plant growing on the edge of a river was partly submerged by a dune. The stem was examined to find the difference between the submerged and the aerial parts.

	Submerged	Aerial
Cortex and phloem	400 μ	380 μ
Wood cylinder	836	950
Pith	1976	1482
	3212	2812

The upper exposed part is not as large as the submerged part, but the wood cylinder is larger.

	Submerged	Aerial
N.	62	44
D.	23	38
W.	2.3	3.2
F.	5.1	5.6
L.	10.4	5.6

In a given area in the cylinder there are fewer vessels, larger in diameter but less in area, which must be more than compensated for by the size of the whole cylinder. The walls of the vessels and fibers are heavier and the lumina of the fibers smaller, giving more wood.

SALIX LONGIFOLIA

Situation the same, but the parts examined were not parts of the same stem, but were of the same size.

	Submerged	Aerial
N.	42	51
D.	41	43
W.	3.2	2.4
F.	3	3.2
L.	7.7	6.8

In aerial stem more and larger vessels, walls slightly thicker, lumina of fibers smaller, giving more wood.

The swamp forms on the whole show the same variations as the mesophytic forms.

Table (I) on p. 298 gives a comparison of mesophytic and dune forms of the same species with respect to eleven characters of the leaf.

A summary of leaf characters is as follows:

Hairs more abundant	12 *X*	(3 same)
Surface of upper epidermal cells greater	9 *X*– 5 *M*	(2 same)
Depth of upper epidermal cells greater	5 *X*–12 *M*	(4 same)
Side walls of upper epidermal cells wavy	6 *X*–11 *M*	
Side walls of lower epidermal cells wavy	8 *X*–16 *M*	
Outer wall of epidermis heavier	18 *X*	(2 same)
Cuticle ridged	10 *X*– 6 *M*	
Palisade more completely organized	17 *X*	(1 same)
Better development of conductive elements	15 *X*– 2 *M*	(1 same)
Heavier sclerenchyma	14 *X*– 1 *M*	(1 same)
Heavier collenchyma	17 *X*	

All leaves, with the exception of those of *Populus balsamifera*, were thicker in the dune form than in the mesophytic. The poplar was growing alone at the side of a road, so the exposure was greater than in the woods where most of the mesophytic specimens were collected. The bud scales also were thicker, and in most cases the outer wall, or the cork if it had developed, was thicker.

The greater extent of surface in the upper epidermal cells in the majority of the dune forms is striking. GREVILLIUS speaks of epidermal cells in the alvar plants being smaller than in the normal, but he may have used the lower surface only, as he mentions the subject in connection with stomata, and that may differ from the upper surface. Cuticular transpiration is reported as taking place from the side walls of the epidermal cells more abundantly than from the lumen of the cell. If this is true, then increase in the surface extent of the cell would decrease cuticular transpiration. The apparent thickness of the epidermis of dune forms is due to the heavy wall and cuticle and not to the depth of the cells. Waviness of the side walls seems to be related to shade, as it occurs more frequently in mesophytic leaves, and in mesophytic leaves on the under side. Ridging of the cuticle accompanies great thickness. Deep, compact palisade, well developed conductive elements, heavy sclerenchyma, and the presence of hairs are characters noted

TABLE I

LEAF CHARACTERS OF MESOPHYTIC AND DUNE FORMS COMPARED

	Acer	Asclepias	Celastrus	Celtis	Cornus	Fraxinus	Juglans	Liriodendron	Ostrya	Populus balsamifera	Populus deltoides	Prunus virginiana	Psedera	Ptelea	Rhus	Salix longifolia	Smilacina	Smilax	Tilia	Ulmus	Vitis
Hairs more abundant	x	x	o		x	x	x	o		mx	x	x	mx	x	x	o	x	o	mx	x	x
Surface of epidermal cells absolutely greater	mx	x	x		m	m	mx	m			m	x	x	x			x	x	x	m	x
Depth of epidermal cells relatively greater	m	m	mx	mx	m	x	m	m	m	x	mx	m	m	mx	m	x	m	x	m	x	m
Side walls of upper epidermal cells wavy	mx	o	mx	m	m	mx	m	m		o	o	mx	o	m			mx	mx	o	m	o
Side walls of lower epidermal cells wavy	mx	mx	mx		m	mx	m	m		m	o	mx	m	m			mx	mx	m	m	mx
Outer walls of epidermis (including cuticle) heavier	x	mx	x	x	x	x	x	x	x	x	x	x	x	x	x	x	mx	x	x	x	
Cuticle ridged	x	mx			x	x				x		x	m	mx				x	mx	m	mx
Palisade more completely organized	x	x	x	x	x	x	x	x	x		x	x	x	x	x	mx			x	x	x
Better development of conductive elements		x	x	x	x	x	x	x		x	x	x	m	mx	x		x	m	x	x	mx
Heavier sclerenchyma	x					x	x	x	x	x	x	x	x	x	x	x	x	m	mx	x	
Heavier collenchyma		x	x	x	x	x	x	x			x	x		x	x	x	x	x	x	x	x

in true dune plants and generally admitted to be xerophytic. Stomata appear only on the under sides of leaves of both forms except in the cases noted, where they appear on both sides; there is no variation except in the one tree *Ostrya* which sometimes has stomata on the upper surface also. Occasionally specimens from mesophytic situations in the dunes show interesting variations. In these places a great deal of humus has collected above the sand, changing the water content and other soil relations, and xerophytic pioneers have made enough shade and protection for mesophytic forms to come in, so woods have developed. The exposure must be less here and the water relations better than on dunes with scantier vegetation, yet leaves of *Fraxinus*, *Cornus*, and *Ostrya* collected in these woods were thicker than some of the dune forms. The internal structure of *Fraxinus* differed from the dune form, the palisade consisting of a single layer of cells, not compactly arranged.

Another interesting variation comes out in the comparison of leaves of different seasons. Those collected in 1911 are frequently thicker than those collected in 1909 in the same habitat, so that the mesophytic form of 1911 is sometimes thicker than the xerophytic form of 1909, but the xerophytic form of 1911 is correspondingly increased. The season was an unusual one, showing temperatures of 39°, 46°, and 66°, for March, April, and May, in which time the leaves became fully mature, the normal being 34.4°, 45.9°, and 56.5°. In 1909 the temperature was very near the normal. The normal percentages of possible sunshine are 52, 60, and 64, while 1911 had 63, 54, and 79, so March and May were considerably above the average, though April went below. Precipitation was near the normal except in March, when it was only a little more than half. Winds were not unusually high. The variation in thickness must have been due, at least in part, to the unusually high temperature in the three months, sunshine above the average in March and May, and small precipitation in March.

The accompanying table (II) gives a comparison of mesophytic and dune forms as to nine characters of the stem.

TABLE II

STEM CHARACTERS OF MESOPHYTIC AND DUNE FORMS COMPARED

	Acer	Asclepias	Celastrus	Celtis	Cornus	Fraxinus	Hamamelis	Juglans	Liriodendron	Ostrya	Populus balsamifera	Populus deltoides	Prunus virginiana	Psedera	Ptelea	Rhus	Salix longifolia	Smilacina	Smilax	Tilia	Ulmus	Vitis
Vessels more numerous	*m*	*m*	*x*	*x*	*x*	*m*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*mx*	*m*	*m*	*m*	*m*	*x*	*x*	*x*
Vessels larger	*x*	*x*	*m*	*mx*	*x*	*m*	*m*	*m*	*m*	*m*	*m*	*x*	*m*	*m*	*x*	*m*	*x*	*x*	*x*	*x*	*mx*	*m*
Total area of vessels larger	*x*	*m*	*m*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*m*	*x*	*m*	*x*	*m*	*x*	*x*	*x*	*x*
Walls of vessels heavier	*x*	*x*	*x*	*x*	*x*	*x*	*m*	*x*	*x*	*m*	*m*	*x*	*x*	*x*	*x*	*x*	*mx*	*mx*	*x*	*x*	*m*	*x*
Walls of wood fibers heavier	*x*	*x*	*m*	*x*	*x*	*x*	*x*	*m*	*x*	*x*	*m*	*x*	*mx*	*x*	*x*	*x*	*x*	*x*		*m*	*m*	*m*
Lumen of fibers smaller	*m*	*x*	*x*	*x*	*mx*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*m*	*x*		*x*	*m*	*mx*
More growth rings in stem of given size	*m*		*m*	*mx*	*x*	*m*	*x*	*mx*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*m*	*m*		*mx*	*m*	*x*
More sclerenchyma and collenchyma	*m*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*m*	*m*	*x*	*x*	*x*	*m*	*x*	*m*	*mx*	*m*
Cork thicker	*m*		*m*	*m*	*x*	*x*	*m*	*m*	*x*	*x*	*x*	*x*	*x*		*x*	*m*	*m*			*m*	*mx*	*x*

A summary of stem characters is as follows:

Vessels more numerous	14 *X*– 7 *M* (1 same)
Vessels larger	9 *X*–11 *M* (2 same)
Total area larger	17 *X*– 5 *M*
Walls of vessels heavier	16 *X*– 4 *M* (2 same)
Walls of fibers heavier	14 *X*– 6 *M* (1 same)
Lumen of fibers smaller	16 *X*– 2 *M* (2 same)
More growth rings	10 *X*– 6 *M* (3 same)
More sclerenchyma and collenchyma	15 *X*– 6 *M* (1 same)
Cork thicker	9 *X*– 8 *M* (1 same)

There is a tendency for the vessels to be larger in the mesophytic forms, but more numerous in the xerophytic, the area being greater in the xerophytic. A greater number of xerophytic forms have heavier walls of vessels and fibers and smaller lumen in the fibers, making a more woody cylinder. A majority of xerophytic forms have more growth rings to the given diameter than the mesophytic forms, showing slower growth under the more adverse conditions. A majority of xerophytic forms show an increase in mechanical tissue as well as in the wood and an increase in cork formation, though this is not so marked as one might expect. The internodes in the stem, in every case measured, were shorter in the xerophytic form.

The lianas seem more apt than the trees to show exceptions to the general stem situation. Their vessels are always extraordinarily large, but why they should often be larger and more numerous in mesophytic forms, when those of trees are not, is impossible to guess.

Discussion of theories

That the characters cited are due to the conditions under which the plants live, or have lived in the past, is undoubted, but what are the immediate causes remains to be proved by experiment. The purpose of this investigation has been to get at a few facts, but it may be of some interest to review a few of the theories:

Mrs. Clements (**4**) considered light the principal factor in the development of deep palisade. Haberlandt (**16**) said that light does not influence the structure of this tissue but only its disposition, and that the reason palisade is developed is because

the products of assimilation ought to be carried away from the assimilatory cells by the shortest possible road, and the form of cells best fitted for this rapid transportation is the elongated form. WAGNER (**29**) reported that alpine plants exposed to decreased transpiration did not show a reduction in palisade, and concluded that not transpiration but assimilation was more effective in producing that tissue. PICK (**25**) thought the elongated form of the palisade is ancestral, but that for a strong development light is necessary; DUFOUR (**9**) agreed with him in this respect. STAHL (**26**) related palisade development to light. EBERDT (**10**) thought that increase in palisade development is caused by assimilation and transpiration working together, and that light in itself is never the cause that calls forth palisade parenchyma. VESQUE and VIET (**27**) concluded from their experiments that light and dry air (accelerating transpiration) result in a greater development of palisade. BONNIER (**2**) adds temperature to these two factors. KEARNEY (**22**) considers excessive transpiration accountable for both increased palisade and succulency. HEINRICHER (**20**) related equilateral structure to the vertical position of leaves and thought it due to sunny and dry situations, dryness being secondary to strong illumination, as some plants growing in damp situations have equilateral leaves.

As to conductive and mechanical elements, it has long been known that they are reduced in aquatic plants, in the water leaf of *Proserpinaca* being scarcely differentiated at all. If the supply of water is the limiting factor, one would expect an increase in these tissues the more xerophytic the conditions; but of course water is not the only factor, and with the plant out of water, its roots in the soil, its leaves in the air, the larger the plant, and consequently the farther apart the roots and leaves, the more complicated become the factors. GILG (**14**) found in the xerophytic family Restiaceae a mechanical ring of strongly thickened cells, which VOLKENS (**28**) explained as related to poor water supply. HABERLANDT (**17**) thought mechanical influences, if they do not pass beyond a certain limit, act on stereome as a stimulus for further building it up. KOHL (**23**) found that in some plants grown in damp air the sclerenchyma ring was entirely lost, xylem elements

less numerously developed, and bast bundles weak or gone, due, he said, to differences in activity of transpiration. JOST (**21**) found that in *Phaseolus* a great mass of vessels was formed, even if transpiration was reduced to the minimum, and says "transpiration can indeed influence the quality and quantity of the vessels, but is not the cause of their formation. If it were so, the stems of our trees would grow in thickness as long as they transpire, at least the whole summer through, which they do not do." HABERLANDT (**18**) relates the number and size of the ducts to the transpiring leaf surface. HARTIG (**19**) agrees with HABERLANDT and adds "in the damp air of a dense forest the inner spaces are much narrower than in an open stand." PFEFFER (**24**) considers that within certain limits the development of the conducting system is favored when an increased demand is made upon it. VOLKENS (**28**), in studies of desert plants, found a small development of water-conducting elements. CANNON (**5**) irrigated desert plants and compared their ducts with those of non-irrigated plants and found better development in the latter. The two results may not be inconsistent. VOLKENS' plants may have reduced leaf surface or developed succulency, thus reducing transpiration, and so in a way correspond with CANNON'S irrigated plants.

Conclusions

Conditions in the dunes are severe for plant life, including direct illumination and reflection, extremes of temperature, strong winds, sand-blast, and sandy soil, the result of all these factors being increased evaporation. The presence of considerable water above the water-table makes conditions less severe than they otherwise would be. The response to these conditions by true dune plants is seen in the predominance of low vegetation, long roots, woody stems, thick leaves (which may be reduced, equilateral, evergreen, or folded), succulency, hairs, thickened epidermis and cuticle, deep palisade, sunken stomata, and well developed mechanical and conductive tissues in all parts.

Plants generally growing in mesophytic situations, when found also on the dunes, show the following modifications: *of the leaf*, increased thickness, decrease in depth and increase in surface-

extent of epidermal cells, increase in thickness of the outer wall of the epidermis and of the cuticle accompanied by ridging, increase in palisade, in hairs, in conductive and mechanical tissues; *of the stem*, decrease in the length of internodes, increase in the number of vessels and in the area of their cross-sections, giving greater conductive space, increase in thickness of the walls of vessels and of the fibers accompanied by decrease in lumen of fibers, giving more wood, increase in the number of growth rings in stem of a given size, showing slowness of growth, increase in mechanical tissues outside the wood, and increase in cork.

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PARNASSIA AND SOME ALLIED GENERA

LULA PACE

(WITH PLATES XIV–XVII)

The systematists have had some trouble in classifying *Parnassia*. In an old Westphalian Flora by KARSCH (**15**) it is placed in the family Droseraceae. HALLIER (**12**), in discussing the Saxifragaceae, says *Parnassia* is much more closely related to the Droseraceae than to the Saxifragaceae; while EICHINGER (**6**) concludes that it should be placed with the Saxifragaceae as ENGLER (**8**) has it. WETTSTEIN (**26**) also places it there and takes Droseraceae out of the Sarraceniales and puts it with Parietales. The possibility of finding some characteristics that would help settle this question led to the present study. CHODAT (**3**) has used *Parnassia* to illustrate certain stages in the development of the embryo sac and embryo of angiosperms.

The work was undertaken at the suggestion of the late Professor STRASBURGER, and his continued advice was of the greatest service.

Parnassia palustris

MATERIAL.—The material which had been collected in Switzerland, and in the neighborhood of Bonn, Germany, was kindly placed at my disposal by Professor STRASBURGER. It had been killed in an alcohol acetic mixture (three parts of alcohol to one part of glacial acetic acid). The usual methods were followed in preparing the material for cutting. The younger stages were cut 5–6 μ thick and the older 8–10 μ. The triple stain, safranin-gentian violet-orange G, was most satisfactory, but iron-alum hematoxylin alone and with Congo red was also used.

The parts studied showed very few irregularities, or so-called abnormalities. Out of several hundred ovaries sectioned, the majority had five placentae, a few had four, two had three, and one had only two; in the last the two placentae were not quite normal in appearance. One ovary had a very irregular structure; it was as if the carpels had not grown together, and more or less

perfect anthers, containing apparently normal pollen, were found on these (fig. 70). One anther had developed on a staminodium; two anthers were normal in appearance. CHAMBERLAIN (**2**) has reported certain somewhat similar irregularities in anther development in *Salix*.

MEGASPORES.—A complete series in the development of the ovule from the first protuberance was studied. The earliest stages show no differentiation of sporogenous tissue. The first difference to be noted is in ovules that are somewhat advanced; and these show only a difference in the size of the cells, there being no definite arrangement of these and no difference in staining reaction. Certain characteristic groups of these larger cells are shown in figs. 1, 2, and 3; the first two are from the same section. Often there are only two large cells, as may be seen in fig. 1, but in this case a third cell is below these two. Fig. 2 has four large cells that evidently were produced from one cell by two successive divisions, thus giving a rather striking resemblance to four megaspores; the wall between the two upper cells is very faint. At this stage, if the section is not perpendicular to the wall, one gets the impression of two nuclei without a separating wall, as CHODAT (**3**) has shown in his fig. 660; but I found no case in which the wall was really lacking. Fig. 3 is an ovule with one of the large cells in mitosis, showing the 20 chromosomes of the diploid generation. The ovule is somewhat larger before the difference in staining reaction appears, and the difference in the size of the cells is also more striking (fig. 4).

The inner integument begins to develop at this time. Fig. 5 has both integuments and the sporogenous cell is in synapsis. Synapsis was not found in younger ovules, but apparently it continues for some time, as it was often found in much older ovules, judging by the development of the integument. CHODAT'S fig. 660, *c* (**3**), is similar to fig. 5, except that he shows the nucleus without other contents than the nucleolus. Only a few instances were found in which more than one cell showed both by size and staining reaction the sporogenous characteristics. Fig. 6 gives two sporogenous cells, the cell with the nucleus in synapsis being much the larger. In fig. 7 the cells are approximately the same size, but the section was cut so that one cell was unfortunately directly over the other. Here

the cell in synapsis is somewhat shorter and broader than the other. The walls of one cell are dotted in, but the walls of the other and both nuclei are drawn.

The mother cell divides in the usual manner (figs. 4, 8, 9). A full series was studied, but only a few drawings will be shown. In fig. 5 the synapsis stage is shown and in fig. 8 the spirem. The chromosomes are quite short and thick in fig. 9, and the haploid number (10) can be counted. The daughter cells sometimes differ slightly in size, but as a rule the difference is not marked (fig. 10). In fig. 11 the lower daughter cell has the spindle already formed for the second division, while the upper daughter cell has only formed the chromosomes, the nuclear membrane being still complete and very distinct. But in fig. 12 both daughter nuclei are in the early telophase of this division. In the upper cell one chromosome did not reach the pole and was left out of the megaspore nucleus. This condition was seen only a few times; and, as the upper megaspore always disintegrates in the material studied, it does not seem to be of any importance in the life-history of this plant. One example of the same condition was found in the first division. Here it might affect the life-history; for very often the second megaspore develops. If the nuclei continued to divide as usual, this might give an egg with one less than the usual number of chromosomes, in this case 9 instead of 10.

Figs. 13–15 show the different positions of the megaspores, a straight row in fig. 13, the two lower in a row and the two upper side by side in fig. 14, and approaching the tetrad form in fig. 15. CHODAT (**3**) gives in his fig. 661 a straight row of four megaspores and in fig. 662 a row of three cells; in both cases the lower megaspore has enlarged to produce the embryo sac.

EMBRYO SAC.—While in angiosperms it is probably true that the lowest of the four megaspores usually produces the embryo sac, the others disintegrating, cases showing that any of the four may function have been reported, and in some instances all four show sac tendencies. COULTER and CHAMBERLAIN (**4**, p. 84) give a summary of the literature on this subject. In *Parnassia* apparently the second or the third as frequently develops as the fourth (figs. 16–29), but no case was found in which the first developed. These

figures show that often two of the megaspores begin to develop, apparently either two of the lower three, second and fourth (figs. 16–18), second and third (fig. 17), third and fourth (figs. 22 and 24). In fig. 25 one of the two upper adjacent megaspores and the fourth one began to develop, but the upper one is in the best condition, the fourth one being less dark than the other two, but darker than the upper one. The epidermis is quite pale over this spore. Fig. 23 has the appearance of five megaspores, but one nucleus is quite small with apparently only one chromosome, and is probably the result of an abnormal division like that shown in fig. 12.

The epidermal layer of the nucellus begins very early to disintegrate. These cells nowhere had the usual appearance of disintegrating cells. As is well known, cells disintegrating under apparently similar conditions stain deeply and have a more or less crushed or squeezed appearance. But here they seem to grow paler, as if the cytoplasm within them were diminishing, and finally all contents disappear. Later the walls also are more or less completely absorbed. An attempt to show this is made in figs. 24, 26, 27. In fig. 24 the whole epidermal layer is pale almost to the base of the fourth megaspore; in figs. 26 and 27 the cells are disappearing from the upper part of the nucellus, leaving the megaspores lying next to the inner integument. The disintegration in this region continues until only the lower end of the sac is inclosed by nucellar tissue, the greater part of it being in contact with the integument and having no cells between it and the micropyle (figs. 30, 31, 33–36). CHODAT'S (**3**) figs. 661–666 show this disintegration of nucellar tissue. He says:

> Chez beaucoup de Gamopétales et ches quelques Dialypétales la mégaspore qui s'est développée dans un très petit nucelle dissont le sommet de celui-ci et fait saillie an dehors dans le micropyle.

The disorganization of this layer of cells may furnish food to the upper megaspores and thus give them a better chance to develop than they would otherwise have. On the other hand, it is altogether possible that this disintegration is due to the unusual activity of these megaspores.

Fig. 27 shows a two-nucleate sac that developed from the second megaspore; the third megaspore is quite large and as yet shows no

signs of disintegration. The fourth megaspore is fast disorganizing, being a darkly stained almost structureless mass. The first megaspore and the nucellar layer over the upper part of the sac show only traces of their former existence. An embryo sac developing from the fourth megaspore is shown in fig. 28. The nucleus is in mitosis for the first division, and the 10 chromosomes can be counted. The three upper megaspores are completely disorganized, and the nucellar cells near the micropyle are paler and with very little contents. The vacuole appears early in the two-nucleate sac (fig. 29). It is not common to find the second and the third megaspores persisting so long as they have here. The two upper nucellar cells have very little cytoplasm in them and stain much lighter than the others.

In fig. 30 an entire ovule at a little later stage is shown with less magnification. The nucellar layer has disappeared completely from around the upper part of the sac, leaving it in contact with the inner integument and an open micropyle all the way to the sac. The only part of the nucellus remaining is that below the lower nucleus of the two-nucleate sac. It is interesting to note that SHREVE (**20**) has shown a similar figure for *Sarracenia*, all the nucellar tissue except that at the base having been destroyed. The loose, spongy tissue is already appearing in the chalazal end of the ovules. This becomes very conspicuous in older stages.

Figs. 31 and 32 show the second mitosis in the embryo sac. In one nucleus of each sac it is possible to count the 10 chromosomes. In the first the chromosomes have been formed in both nuclei, in the second only in the lower one; the upper one has the spirem very thick and short and probably shows the early stages of segmentation. In both ovules the nucellar layer has disappeared from the upper half of the sac. The spindles for the second division are at right angles to each other (fig. 33). This sac developed from the second megaspore, and in this case the third one has also begun to develop. Fig. 34 shows a four-nucleate sac with the chromosomes more or less completely segmented for the third division. The nucellar layer has disappeared from the upper two-thirds of the sac. The inner layer of cells of the integument is shown on one side of the sac in fig. 35. The sac nuclei are in the late anaphase of the third division. The upper spindle is almost perpendicular to the paper,

and so it is not easy to show it correctly. Each of these spindles shows the thickening of the spindle fibers in the center, characteristic of early wall formation, but further development of the walls does not take place, as is shown in fig. 36. The nucellar layer is represented by a more or less distinct line of stuff which can be traced to the perfect cells below the sac. The darker thicker mass near the micropyle is probably the remains of the megaspores.

The eight nuclei arrange themselves in the usual fashion (fig. 37). In this figure the egg lies just back of the synergids and only the lower part of it is shown in the drawing; and the polars are almost in contact. Here the large nucleoli characteristic of these nuclei are well shown, the nuclei having very little other stainable material in them. In this case practically all of this material is shown in the drawing, which was made not with a single focus, but by focusing in all parts of the nuclei. At any given focus one's first impression of the nucleus is an empty circle except for the very large nucleolus. The inner layer of cells of the integument is drawn on only one side of the sac. This layer has the appearance of the so-called tapetum or jacket layer formed in many of the Sympetalae, as well as in other forms, and is quite different in appearance from the adjacent cells. CHAMBERLAIN (1) has shown it in *Aster novae-angliae*. EICHINGER (6) says:

> Bei unserer *Parnassia* kann man füglich von einem Tapetum nicht sprechen, die innersten Zellen des Integuments unterscheiden sich nicht allzusehr von den andern.

But in my material the difference in shape and staining was striking.

Small vacuoles are already present in the synergids. One synergid shows the beginning of the indentation, *Leiste* of STRASBURGER (21), which in later stages gives a caplike appearance to the upper part of the synergid. It seems to be related to the cytoplasm of the sac, that is, it is always just where the cytoplasm of the sac reaches its highest point of contact with the synergid. It seems probable that, as the filiform apparatus develops (being of cellulose, it is somewhat stiff) and the synergids elongate, this upper stiffer part does not change shape so much as the lower part. A filiform apparatus is common in angiosperms, but it is not always so strikingly developed as here. In *Die Angiospermen und die Gymno-*

spermen (**22**), STRASBURGER shows (pl. 2, fig. 19) a filiform apparatus, but no notch in *Polygonum divaricatum*. COULTER and CHAMBERLAIN (**4**, p. 94) say that "such beak-like extensions of the sac and synergids are usually associated with narrow and long micropyles." But in *Parnassia* the micropyle is usually wide open and even all nucellar cells have disappeared from this region.

A similar filiform apparatus and notch are shown by STRASBURGER (**21**) in *Santalum*. This is shown quite clearly in spite of the very imperfect technique of that time. In *Santalum* the notch seems to be definitely related to the embryo sac wall, the upper part of the synergids protruding beyond the wall, and this indentation being just against the upper end of this broken wall. NAWASCHIN (**16**) shows in his fig. 9 a very deep notch in the synergids of *Helianthus annuus*. The synergids are pointed, but do not show the lines of the filiform apparatus in the upper part, although just below the notch the lines are quite distinct. This part of the figure is not described, and it may be that the upper part has the usual lines of the filiform apparatus, but they failed to appear in the plate. Here the notch seems definitely related to the cytoplasm of the sac, very much as it is in *Parnassia*. JUEL (**14**) shows the usual embryo sac in *Saxifraga granulata*, but does not describe a filiform apparatus. This stage he shows in a microphotograph which is quite indistinct in this region. Fig. 38 is slightly older; the filiform apparatus is beginning to develop in the synergids. The nucleus is above the vacuole in one and below it in the other synergid. Fig. 39 has an unusual development of the vacuoles in the synergids; here the polars are in contact. In fig. 40 the vacuoles are below the nuclei in both synergids, and the polars have fused, forming the primary endosperm nucleus. The filiform apparatus and notch are quite distinct by this time. Another view of a sac of about the same stage is shown in fig. 41. In this ovary many sacs were still in the four-nucleate condition.

The upper part of a mature sac is shown in fig. 42. The polars have already fused. In *Parnassia* they apparently always fuse immediately, as they are fused in all the mature sacs examined. The caplike filiform apparatus is always very conspicuous at this stage, and stains red with Congo red, which shows it to be cellulose. The

inner row of cells of the integument next to this part of the sac is disintegrating, the disorganization being more or less complete as far down as the last cell drawn, which seems to be still active, as both nucleus and cytoplasm have the usual staining reaction and structure of active cells. Fig. 43 is the other view of a similar sac, being cut at right angles to that of fig. 42; the other synergid is directly under the one drawn. Here the egg apparatus is farther up in the micropyle, and a few of the cells of the integument over the filiform cap have entirely disappeared. CHODAT (**3**) shows an embryo sac before and after fusion of the polars in his figs. 664 and 665, but does not show the filiform apparatus of the synergids. His fig. 677 suggests the possibility of its presence, but does not show it clearly. The pollen tube is just below it.

In many ovules the egg apparatus is entirely in the micropyle, a few of the cells of the integument being disorganized in most instances (fig. 44). The whole egg apparatus has the appearance of being squeezed into a space too small for it. The polars have fused. In fig. 45 the synergids lie one above the other in the micropyle, the egg being just at its entrance. These synergids show the notch and the filiform appearance quite distinctly. If the synergids are not entirely separated, they may have somewhat the appearance of pollen tubes; but it is always easy to distinguish them from the latter by the difference in staining reaction, and by the fact that the real tube structure is lacking. A diagram with less magnification (fig. 46) shows the whole upper portion of the ovule. Fig. 47 shows one synergid nucleus just at the entrance of the micropyle, some of the cytoplasm of this synergid being entirely outside of the ovule. In fig. 48 the entire egg apparatus is just at the entrance to the micropyle, with the polars in contact in the upper part of the sac. A few ovules were seen in which the whole of the egg apparatus was entirely outside of the micropyle. These figures with the synergids in the micropyle are very similar to the structures shown by CHODAT (**3**) in his figs. 675–676, which he calls pollen tubes.

POLLEN.—The anthers present the usual four-lobed appearance, with four sporogenous regions. A group of mother cells in more or less perfect synapsis is shown in fig. 49. After synapsis there is a thick spirem which segments into 10 chromosomes (fig. 50). The

telophase is shown in fig. 51. The chromosomes seem to remain distinct here (figs. 51 and 52) and could often be counted after the nuclear membrane was formed. Fig. 53 shows the metaphase of the homotypic division; the two spindles being almost at right angles, one nucleus is cut exactly at the plate and the other shows almost all of the spindle. The formation of the tetrad is shown in fig. 54. Different views of the microspores soon after their formation are shown in figs. 55 and 56. The nucleus divides at once to form the tube and generative nuclei (figs. 56–59). The wall apparently disappears early, as several gametophytes without a wall separating the two nuclei were found in these same anthers. The stages shown in figs. 55–59 come from the same anthers, all the anthers of this flower being in the same stage.

FERTILIZATION.—The pollen tube comes through the micropyle, which is usually open (figs. 30, 42, 43), curves around the tip of the synergid, and seems to empty into one of the synergids below the notch (fig. 60). In this sac the other synergid is quite dark, and the tube can be traced to this dark mass. Fertilization has already taken place, and there are two endosperm nuclei. In fig. 61 the same dark appearance of one synergid is found, and again the other synergid is unchanged. Fusion of the sex nuclei has already taken place; both the egg and the primary endosperm nucleus show much more chromatin than they do in the mature sac (fig. 43). Several pollen tubes were seen, all about the same stage. Only one more will be shown (fig. 62). In this the bending of the tube around the upper part of the synergid is not so clearly shown, as the section was not so fortunate in position as that in fig. 60, yet the tortuous course is quite evident. But especially clear is the emptying of the tube into one synergid. The contents of this synergid consist of a very darkly stained mass in which no structure can be distinguished except one nucleolus, which is quite clear because of its bright red color in the dark purplish mass. It is probably the nucleolus of the synergid nucleus. The other synergid is in the next section and is quite normal in every respect.

GUIGNARD (**11**) in *Nicotiana Tabacum* and *Datura laevis* reports the pollen tube passing into one synergid and discharging its contents there. JUEL (**14**) has described a similar passing of the

contents of the pollen tube into one synergid in *Saxifraga granulata*. CHODAT (**3**, p. 552) says:

> Lorsque le noyau fécondant est entré dans le sac on remarque qu'au moins l'une des synergids perd sa turgescence et se désorganise.

In his fig. 677 he shows a pollen tube which from the drawing might be either inside or outside of the synergid. In this mass are three nuclei, one evidently the synergid nucleus. Fig. 63 shows a sperm cell in each synergid. There seems to be a distinct layer of fine-grained cytoplasm about each of these nuclei. One synergid also has another somewhat irregular mass of nuclear stuff which is probably the tube nucleus. This sac was cut slantingly, so that the micropyle and filiform apparatus were in another section, but no trace of the pollen tube was found in this region. Another ovule in the same section had an embryo of five cells. But only a very few embryos were present in this ovary, and the other ovules did not show evidence of fertilization; so that probably only a few pollen grains had reached the stigma. These two dark synergids, each containing a sperm cell, might be interpreted as evidence of two pollen tubes in the same sac. But as there is no other trace of pollen tubes or other nuclei, and the egg and primary endosperm nucleus do not have the appearance of having been fertilized, it seems best to suppose that only one pollen tube has entered and that it burst just where the two synergids are in contact. In this way it would be possible for part of the contents to pass into one synergid and part into the other. Both synergids are quite dark and show little trace of vacuoles, which are quite conspicuous in mature sacs.

NAWASCHIN (**16**) says that after the pollen tube passes the micropylar canal and the nucellus of the ovule, and its tip is in contact with the embryo sac, one of the synergids bursts and pours part of its contents into the micropyle. This forms a half-empty tube of this synergid, and the sudden diminution of pressure causes the pollen tube to burst and its contents are poured out next to this synergid into the sac. Then the sperm nuclei begin active movement toward the depression in the "Endospermanlage," and move from there to the female cells. In *Parnassia* it is very evident that the pollen tube passes around the tip of the synergid without either

synergid or pollen tube bursting, and that the tube empties into the synergid just below the notch. This process itself was not seen, as unfortunately all my material was too old to show this, even fertilization having already taken place in every case except one. But the pollen tubes themselves were unusually clear; they could often be traced through the entire micropyle to the point where they entered the synergid. CHODAT (**3**) shows the sex nuclei in various stages of fusion in his figs. 678–680.

EMBRYO.—One and two-celled embryos showed nothing unusual. The endosperm nucleus usually divides first; only one exception to this was seen (fig. 65). Here there is a five-celled embryo with the endosperm nucleus still undivided and somewhat amoeboid in shape, which is also unusual in *Parnassia*. One sac was seen with a two-celled embryo and two endosperm nuclei, one near the embryo and the other near the antipodals, and one synergid still perfect. Empty pollen tubes are often very persistent in *Parnassia*. It is not uncommon to find a pollen tube that can be seen through the greater part of the micropyle and with the curve at the entrance to the sac where it passes around the beak of the synergid, but with little trace of the synergids below this, when the embryo has 20 or more cells. In the second division in the embryo, the upper cell again divides in the same plane as the first division, while the lower cell divides at right angles (fig. 64). Fig. 65 shows the five-celled embryo. Not many embryos of this stage were seen, but this seems to be the usual arrangement of cells. Fig. 66 gives the next stage, where the upper cell had again divided in the longitudinal direction. In fig. 67 the dermatogen is differentiated, and a layer of endosperm about two cells in thickness extends entirely around the sac next to the wall; in the center are a few free nuclei. Soon the plerome and periblem are also differentiated, as can be seen from the end of the embryo in fig. 68. This entire embryo is outlined in fig. 69 and the plerome is dotted in. The two cotyledons are already formed, and the embryo now completely fills the upper two-thirds of the sac, except for a layer of endosperm about two cells thick around it. The lower third of the sac is filled with endosperm. CHODAT (**3**) in his fig. 756 shows embryos from the two-celled stage to the differentiation of the dermatogen; his figures 756–775 are similar to my figures 75 and 81.

Saxifraga

Several species of *Saxifraga*, growing in the Botanical Garden in Bonn, were examined, to be sure that the usual form of this genus was known. The same methods of fixing and staining were used for *Saxifraga*, *Heuchera*, and *Drosera* as had been employed with *Parnassia*.

JUEL (**14**) has given a description of *Saxifraga granulata* which agrees in all the stages shown with the stages here figured; and I have examined *S. ligulata*, *S. sponhemica*, *S. cordifolia*, and *S. crassifolia*, which seem to be so similar that the same figures could be used for each. Not much work was done with the reduction division; but the reduced number of chromosomes in *S. sponhemica* is about 15. JUEL (**14**) found this to be about 30 in *S. granulata*. These two numbers are rather suggestive, especially since GATES's (**10**) investigation of *Oenothera gigas* and STRASBURGER'S (**23**) discussion of this question.

Nothing unusual was seen in the pollen development of *Saxifraga*. The pollen grains are small and with smooth, rather thin walls. It might be of interest to note that in many of the flowers of *S. cordifolia* some of the anthers contained pollen at least twice the usual diameter, and in some cases as much as four times. In one flower this large pollen was found in every other anther, the younger set of stamens all being affected. But not all flowers produced this large pollen, and it was usually irregular in occurrence when present. As all the later flowers were blighted, turning black before the inflorescence was out of the bud, this peculiarity of the pollen was probably due to a fungus; but this was not investigated.

Two young ovules of *S. sponhemica* from the same ovary are shown. Fig. 71 shows the archesporial cell, and fig. 72 a later stage in which there is one sporogenous cell and the primary parietal cell has divided. The mother cell stage is shown in fig. 73, with two parietal cells. In fig. 74 there are three sporogenous cells, only one of which has reached the mother cell stage; a later stage is shown in fig. 75. There are three parietal cells above the mother cell in fig. 76. The whole of this ovule is shown in fig. 79. In *Saxifraga*, so far as examined, the megaspores are always in a row (fig. 78), and the fourth one develops the embryo sac. Not so much material

was examined as in *Parnassia*, but enough to be sure that the development of the other megaspores, if it takes place at all, is not common. The position of the megaspores in the nucellus is shown in fig. 79. Their great depth in the nucellar tissue is in striking contrast to *Parnassia*, where they are immediately below the epidermis, which is disorganizing at this stage.

Fig. 80 outlines an entire ovule with a two-nucleate embryo sac. There are no air spaces, the whole ovule being very compact and much more massive than that of *Parnassia*. The egg apparatus of a mature sac is shown in fig. 81. The synergids have a well developed filiform apparatus and a notch almost if not quite as deep as that in *Parnassia*. A diagram of this entire sac is shown in fig. 82. Two of the antipodals had disappeared. The polars have already fused and the primary endosperm nucleus is near the base of the sac. This seems to be its usual position in *Saxifraga*, at least in the examples I studied. JUEL (**14**) shows it near the middle or toward the antipodal region in *S. granulata* at fertilization. Fig. 83 is a young embryo which has just been differentiated into long suspensor and embryo proper. Two endosperm nuclei are shown.

Heuchera brixoides

This species corresponds so closely with *Saxifraga* that only three figures will be shown. There is usually one mother cell in *Heuchera*. One ovule with two mother cells (fig. 84) is shown, a later stage (fig. 85) with a large amount of parietal tissue, and a mature embryo sac (fig. 86). The placentae of *Heuchera* are like those of *Parnassia*, and quite unlike those of *Saxifraga*.

Drosera rotundifolia

This material was collected near Bonn. ROSENBERG (**19**) has worked out a very interesting chromosome relationship of *D. rotundifolia*, *D. longifolia*, and *D. intermedia*. In his early paper (**18**) he does not figure certain stages which I need for comparison, only quoting from C. A. PETERS (**17**, p. 275):

> Each nucellus produces a sporogenous layer of four cells, but no tapetum. Three cells of the sporogenous tissue soon disintegrate, leaving the fourth, which is the mother cell of the embryo sac and which undergoes subsequent cell division as is usual in angiosperms.

I shall give a few figures, therefore, in order to compare them with *Parnassia* and *Saxifraga*.

The mother cell in synapsis is shown in fig. 87. It will be seen that like *Parnassia* and *Saxifraga* no parietal cells were produced by the archesporium. This is the commonest condition in *Drosera*. But frequently a parietal cell is cut off which divides, as is shown in fig. 88, giving a row of two parietal cells above the mother cell. Occasionally more than one sporogenous cell is produced (fig. 89); but I saw no evidence that more than one embryo sac was produced, or even that more than one cell reached the mother cell stage. The usual row of four megaspores resulting from these two positions of the mother cell are shown in figs. 90 and 91. In some instances the megaspores are not in a row, as ROSENBERG (**19**) has shown in his text fig. 27, *B*, which is similar to fig. 25 in *Parnassia*. So far as examined, only the fourth megaspore develops in *Drosera*. Not so much material was cut as for *Parnassia*, but it is at least certain that the development of the other spores is not common as it is in *Parnassia*.

In *Drosera*, even in the mother cell stage (fig. 87), air spaces begin to develop in the chalazal region of the ovule. These spaces are quite large by the time the embryo sac has reached the two-nucleate stage (fig. 92), and in the mature ovule they are at least as strikingly developed as in *Parnassia*. The embryo sac occupies only the upper third of the nucellus even at maturity, quite in contrast to *Parnassia* and *Saxifraga*. The nucellus also begins to show its peculiar enlargement of cells. The outer layer of nucellar cells, except those directly over the embryo sac, increase enormously in size without increase of cytoplasm or size of nucleus; the latter lies next to the inner side of the cell. This enlargement of the nucellar cells, as well as the air spaces, reduces the specific gravity of the seed. DIELS (**5**) says:

> They are by their constitution capable of floating. HOLZNER states that the seeds of *D. rotundifolia* at a temperature of about 20° are capable of floating for about a month.

In fig. 93 the third division in the sac is shown and enough of the nucellus to show the differentiation in it. In one nucleus the 10 chromosomes may be counted.

The mature sac (fig. 94) has the usual appearance. The synergids have a well developed filiform apparatus and notch. The former is somewhat more dome-shaped than in *Parnassia*, where it is pointed. The synergids are also rather long, reaching almost as far as the lower edge of the egg. The polar nuclei have already fused. Fertilization apparently takes place as in *Parnassia*. The pollen tube passes around the filiform apparatus and seems to enter one synergid (fig. 95). Here probably the fusion of the sex nuclei has already taken place, as only one nucleus can be distinguished in the lower part of the dark synergid and probably another in the still darker mass higher up. Fig. 96 is clearer in this respect. A small bit of the pollen tube can be seen in contact with the filiform apparatus. This synergid is somewhat darkly stained, but still all structures are distinct, the notch and two nuclei; these are the synergid nucleus and the tube nucleus from the pollen tube. The other synergid is very pale and all the lower part has disappeared. The fertilized egg has not yet divided, but the primary endosperm nucleus is in mitosis; the spindle fibers are forming. So far as examined, this nucleus always divides before the fertilized egg in *Drosera*. Many cases were seen with two endosperm nuclei and the egg still undivided.

Discussion

Three other genera of the Saxifragaceae have been more or less completely worked out. EICHINGER (**7**) figures an ovule of *Chrysosplenium* with mature embryo sac that has three layers of nucellar tissue above the sac. In *Astilbe* WEBB (**25**) reports several archesporial cells and one or even two or three megaspore mother cells beginning to divide. The embryo sac is deep in the nucellar tissue, but no filiform apparatus is shown. The embryo has a suspensor of several cells. FISCHER (**9**) in *Ribes aureum* shows ovule development similar to that of *Saxifraga*, except that the filiform apparatus is not shown. TISCHLER (**24**) in a mature embryo sac of *Ribes sanguineum* shows pointed synergids but no filiform apparatus or notch. These cases may indicate that these three genera do not have the filiform apparatus and notch. But it is also possible that the material studied was not at the right age to show these best, or was not cut to the best advantage for these particular structures.

In a recent number of *Das Pflanzenreich* on Droseraceae, DIELS (**5**) says, in discussing relationships:

Die mehrfach den Droseraceen angeschlossene Gattung *Parnassia* wird neuerdings nach dem Vorgang von ADAMSON, ENDLICHER, LINDLEY, und PAYER, allgemein ausgeschlossen nachdem DRUDE in seine gründlichen Erörterung der Frage (Linnaea **39**:293. 1875) auf die gewichtigen Bedenken practischer Natur' hingewiesen hatte, die einer Überführung von *Parnassia* zu den Droseraceen im Wege stehen.

ENGLER (**8**), in a note in connection with the Sarraceniaceae, concludes with these words:

Die Droseraceae nähere sich dadurch in diagrammatische Beziehung manchen Saxifragaceae, von denen *Parnassia* auch allgemein den Droseraceae zugerechnet wurde.

The following is a rather free translation of EICHINGER'S (**6**) summary of the characters which differentiate *Parnassia* from Droseraceae:

1. *Germination.*—*Parnassia* shows normal germination; cotyledons do not function as an absorbing apparatus. The Droseraceae have no primary root; cotyledons have more or less the function of an absorbing apparatus.

2. *Leaf structure.*—The nervature is different. *Parnassia* possesses a typical leaf structure, in the epidermis tannin; the Droseraceae have no typical assimilation tissue and often chlorophyll in the epidermis, and always more or less modified glands.

3. *Flowers.*—All species of *Parnassia* have staminodia; the Droseraceae have not.

4. *Befruchtungsvorgang* (apparently pollination).—It is apparently similar in species of *Parnassia*, has no analogy to the Droseraceae, but has to *Saxifraga*.

5. *Androecium.*—*Parnassia* possesses small simple pollen grains; all of the Droseraceae have tetrads.

6. *Gynaecium.*—*Parnassia* has stalked placentae, a very striking conductive tissue, the nucellus is small-celled and soon vanishes, the embryo is well formed and fills the almost endospermless seed. *Drosera* at least has flat placentae without conductive tissue, characteristically differentiated nucellus, and all of the Droseraceae have small, round, imperfect embryos and much endosperm.

HALLIER (**12**) says:

Under the Saxifragaceae the genus *Parnassia* takes an isolated place. According to its peculiar habit, its low rosette of long-petioled oval leaves, its one-flowered, long, almost leafless flower-stalk, and the lack of hairs, it evidently belongs not to the Saxifragaceae, but in ENGLER'S order Sarraceniales, which, through the frequent appearance of oval, long-petioled, fleshy leaf blades,

long, one or few-flowered peduncle, fleshy, white, oval floral leaves, and its great predilection for wet or moist places, reveals its descent from the relatives of the Nymphaeaceae, and it manifestly has nothing to do with the Saxifragaceae, which are nearly related to the Rosaceae. Apart from the peculiar staminodia, which are evidently morphologically equivalent to the staminodia of many Nymphaeaceae, the fibers (*Fäden*) in the *Rafflesia*, flower, and the corona of *Passiflora*, *Parnassia* fits closely to *Drosera* through its leaf-rosette, its long, almost leafless shaft, the calyx, the five beautiful white petals, the sessile stigmas, the numerous parietal ovules, the method of capsule opening, the small oblong seed, rich in endosperm, and moist habitat. Through its four-leaved (four-carpellate) seed coat it approaches *Nepenthes* also.

A summary of the parts studied by way of comparison may be helpful.

1. The ovule of *Parnassia* and *Drosera* are of the same shape, and both have large air spaces developed. That of *Saxifraga* is very compact and much thicker, and with thicker integuments.

2. In *Parnassia* the archesporium of the ovules is hypodermal and forms no new cells above it. *Drosera* usually develops in the same way, but sometimes there is a single layer of cells between the mother cell and the epidermis. All the Saxifragaceae studied form the archesporium in the same way, but by the time the mother cell stage is reached there are several layers of cells above it.

3. In *Parnassia* the embryo sac comes to lie next to the integument except the very basal portion, all the nucellar cells above and at the side having been destroyed. In *Drosera* the nucellar cells above the sac have a squeezed appearance and are occasionally destroyed completely. At the side and below the sac the layer of cells next the epidermis enlarge very greatly, giving the nucellus of *Drosera* a very peculiar appearance. This may be only another means of decreasing the specific gravity of the seed. The sac of the Saxifragaceae has several layers of nucellar cells above it.

4. All three genera have an enormous development of the filiform apparatus of the synergids, and the notch is also strikingly developed. The filiform apparatus is pointed in *Parnassia* and Saxifragaceae, and less pointed or more dome-shaped in *Drosera*.

5. The primary endosperm nucleus in *Parnassia* and in *Drosera* is immediately below the egg. In *Saxifraga* it is almost in contact with the antipodals, and in *Heuchera* it is far below the egg.

6. The haploid chromosome number in *Parnassia* and in *Drosera rotundifolia* is 10, in *Saxifraga sponhemica* about 15, and in *S. granulata* about 30.

7. In *Parnassia* and *S. granulata* the pollen tube empties into one synergid, and apparently the same is true in *Drosera*.

With reference to the systematic position, EICHINGER (**6**) says that the joining of *Parnassia* to the Droseraceae would completely destroy the unity of this family. Its principal characteristic would be lost. The failure of a primary root, the defective differentiation of the assimilation tissue, the stipular structures, which recall the intra-ovarian scales of many water plants, the numerous secretion glands, the common appearance of cleistogamous and autogamous flowers, the high capability for regeneration, and the appearance of vegetative buds are most important. In *Parnassia* no such relation to water plants is found. If one looks for a suitable place in the system for *Parnassia*, one must admit that it had better remain with the Saxifragaceae. This family has at present so little unity that *Parnassia* makes no break in its systematic characteristics. In discussing the same question, HALLIER (**13**) says: according to the pronounced monocotyledonous type of venation of the sepals and petals, it seems to me to stand not very far from the point of departure of the monocotyledons and as the representative of a separate family, the Parnassiaceae, to belong near the Ranunculaceae, Nymphaeaceae, Droseraceae, and Sarraceniaceae. From the Saxifragaceae, in which ENGLER (**18**) has placed it, it is differentiated by the harp-shaped branching of the veins in the sepals, the large, long *Podophyllum* and *Sarracenia*-like anthers, and the ovule, which has a slender nucellus, as in other relatives of the Saxifragaceae.

After working over my material, I am of the opinion that *Parnassia* is much more closely related to the Droseraceae than to the Saxifragaceae, and that it should at least be put in the same order with the Droseraceae. For as shown above, *Drosera* and *Parnassia* are quite alike in their ovules and in embryo sac development, except as to the nucellus, in which neither is like *Saxifraga*. They differ also in that *Parnassia* has stalked placentae, while *Drosera* has not. *Drosera* has pollen grains in tetrads and *Parnassia*

has them separate. But in neither of these characters does *Parnassia* agree with *Saxifraga*, whose placentae are still more dissimilar and whose pollen grains are perfectly smooth.

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EXPLANATION OF PLATES XIV–XVII

All figures except the diagram in fig. 70 were drawn with the aid of the camera lucida; Spencer ocular no. 4 and 4 mm. objective were used for figs. 5, 30, 45, 46, 47, 48, 67, 68, 77, 79, 80, and 92; ocular no. 4 and 16 mm. objective were used for fig. 69; all others were drawn with ocular no. 4, 1.5 mm. (oil) objective.

The abbreviations used are as follows: *e*, egg; *m*, megaspore; *♂*, male nucleus; *p*, pollen tube; *s*, synergid; *t*, tube nucleus.

Parnassia palustris

FIG. 1.—Young ovule with three large hypodermal cells; two shown in the drawing; the third is just back of these two.

FIG. 2.—A somewhat older ovule with four large cells in a row, evidently derived from a single hypodermal cell by two successive divisions.

FIG. 3.—A different arrangement of the large group of cells, one cell in mitosis, showing 20 chromosomes; from the same ovary as fig. 5.

FIG. 4.—Sporogenous cell differentiated as shown by size and stain; the inner integument is beginning to develop.

FIG. 5.—Synapsis and beginning of outer integument.

FIG. 6.—Two sporogenous cells; the larger one already in synapsis.

FIG. 7.—Two sporogenous cells of approximately the same size; the two cells were in the same section, one lying above the other; the larger cell has the nucleus in synapsis, the other one in an earlier stage.

FIG. 8.—After recovering from synapsis; spirem still very long.

FIG. 9.—Ten short chromosomes; the double character can be clearly seen in several.

FIG. 10.—The two daughter cells with chromosomes formed for the second division.

FIG. 11.—The micropylar daughter cell in same stage as fig. 10; the chalazal daughter cell has nucleus with spindle.

FIG. 12.—Both daughter cells in the telophase stage; in the micropylar cell one chromosome failed to reach the pole and so is omitted from the megaspore nucleus.

FIG. 13.—Four megaspores, apparently all increased in size but the first disintegrating, and the second and fourth larger than the third.

FIG. 14.—A different arrangement of the four megaspores, probably occurring more often than that shown in fig. 13.

FIG. 15.—Approaches still more nearly the usual tetrad arrangement.

FIGS. 16–22.—The variations in the early stages of the megaspores.

FIG. 23.—Apparently five megaspores; one nucleus is very small and seems to have only one chromosome, probably resulting from an abnormal division like that in fig. 12.

FIG. 24.—Third and fourth megaspores developing; the nucellar cells surrounding these are already showing signs of disintegration, and only the three at the base are still normal in appearance.

FIG. 25.—In this case also the epidermal cells are becoming pale, especially over the upper vigorous megaspore, which appears to be more active than the fourth.

FIG. 26.—The third megaspore forming the embryo sac and in mitosis for the first division; the epidermal layer partly disorganized, leaving the sac in contact with the inner integument and an open micropyle.

FIG. 27.—Two-celled sac formed from second megaspore; the third megaspore also developing; the epidermal layer still further disorganized.

FIG. 28.—Embryo sac formed from the fourth megaspore; first division showing 10 chromosomes, the other megaspores represented by a formless mass above; epidermal layer still perfect; integuments well advanced.

FIG. 29.—All the epidermal layer, especially the two upper cells of the nucellus, lighter than the adjacent integument cells; two-celled sac from the fourth megaspore; the second and third megaspores have persisted longer than usual.

FIG. 30.—The entire ovule with two-celled embryo sac; ovule with loose spongy tissue at base; nucellus entirely lacking over greater part of sac.

FIG. 31.—Two-celled sac with nuclei in mitosis for the second division; the 10 chromosomes may be seen in the upper nucleus; the upper half of the sac is in contact with the integument, the nucellus having entirely disappeared from this region.

FIG. 32.—Similar to fig. 31, but the lower nucleus somewhat in advance of the upper; in the lower the chromosomes are short and thick, while in the upper the spirem is segmenting.

FIG. 33.—Spindles for the second mitosis in the embryo sac; this sac developed from the second megaspore; the third megaspore also developing.

FIG. 34.—The four-nucleate embryo sac with the spirems more or less completely segmented for the third division.

FIG. 35.—Spindles for the third division in the embryo sac; in the upper part of the sac one spindle is almost at right angles to the paper.

FIG. 36.—Eight-nucleate sac soon after the third division.

FIG. 37.—Embryo sac soon after the organization of the egg apparatus, the egg being just under the synergids; only the lower part of it with part of its nucleus can be seen; polars not yet in contact.

FIG. 38.—Upper end of sac, slightly older than in preceding figure; one synergid has vacuoles above the nucleus, the other has them below it; the so-called filiform apparatus beginning to be differentiated near the tip of the synergids.

FIG. 39.—From older sac; the synergids have unusually large vacuoles, both above the nuclei; polars are in contact.

FIG. 40.—The polar nuclei have fused; vacuoles below the nuclei in the synergids; the filiform apparatus well developed and forming a caplike structure.

FIG. 41.—This sac was cut at right angles to the one above, showing the whole of the egg, but only one synergid; this ovary still contained four-celled sacs.

FIG. 42.—Upper end of mature embryo sac; the unusual development of the filiform apparatus clearly shown; the inner layer of cells of the integument disintegrating.

FIG. 43.—Same stage as the preceding, but with the egg apparatus still farther up in the micropylar region; some of the cells of the integument entirely disorganized.

FIG. 44.—The entire egg apparatus in the micropyle, the adjacent cells of the integument having disappeared and the egg apparatus having a squeezed appearance.

FIG. 45.—The upper part of an ovule outlined; the egg apparatus in the micropyle, one synergid lying above the other.

FIG. 46.—Egg apparatus in the micropyle, but the synergids so pressed together that it is not possible to differentiate them.

FIG. 47.—A diagram of the upper part of an ovule; one synergid has the upper end entirely out of the ovule, its lower end overlapping slightly the upper part of the other synergid.

FIG. 48.—The entire egg apparatus just at the entrance of the micropyle, giving the appearance of a pollen tube; the polar nuclei are in contact but have not yet fused.

FIG. 49.—A few pollen mother cells; in two of these synapsis is perfect, in the others almost so.

FIG. 50.—The 10 chromosomes may be counted in this pollen mother cell.

FIG. 51.—Telophase of the first division.

FIG. 52.—Telophase of the first division in which the 10 chromosomes are still distinct.

FIG. 53.—Metaphase of the second division, one nucleus showing the spindle and the other being cut parallel with the nuclear plate and showing the 10 chromosomes.

FIG. 54.—The tetrad with a few spindle fibers still present.

FIGS. 55–59.—Stages in the division of the pollen grain into vegetative and generative cells; in fig. 57 the 10 chromosomes are shown.

FIG. 60.—Fertilization: the pollen tube curved around the upper part of the synergid, which is quite dark; apparently the sperm has already fused with the egg; the endosperm of this sac is two-nucleate.

FIG. 61.—The male nuclei have already fused with the egg and the primary endosperm nucleus; the dark mass underneath the synergid and outlined through it is the other synergid and some material from the pollen tube.

FIG. 62.—Pollen tube entering one synergid; the other synergid is just back of this one; fertilization has already taken place; the endosperm nucleus has divided, the other endosperm nucleus being near the antipodals.

FIG. 63.—The upper end of an embryo sac; in each synergid is a synergid nucleus and another smaller dense nucleus (a male nucleus with fine-grained cytoplasm around it); one synergid has a third nuclear mass, the tube nucleus.

FIG. 64.—Mitosis in both nuclei of a two-celled embryo.

FIG. 65.—Five-celled embryo with endosperm nucleus still undivided.

FIG. 66.—An older embryo with traces of a synergid and showing one endosperm nucleus.

FIG. 67.—Older embryo with dermatogen layer differentiated; the endosperm forms a layer about two cells in thickness all around the sac with a few free nuclei in the interior, especially around the lower end of the embryo.

FIG. 68.—The basal part of older embryo, showing dermatogen, plerome, and periblem.

FIG. 69.—The same embryo outlined; a typical straight dicotyledonous embryo which fills about two-thirds of the sac except for the layer of endosperm about two cells in thickness; the other third of the sac is filled with endosperm.

FIG. 70.—A diagram of an abnormal flower; one anther has developed on a staminodium, two are normal, the others, more or less imperfect, are on the carpels, which are not so completely united as usual.

Saxifraga

FIG. 71.—*S. sponhemica:* outer half of young ovule showing archesporial cell.

FIG. 72.—Same: the archesporial cell has divided.

FIG. 73.—*S. crassifolia:* one mother cell.

FIG. 74.—Same: one mother cell, but two other cells are quite large and stain like sporogenous cells.

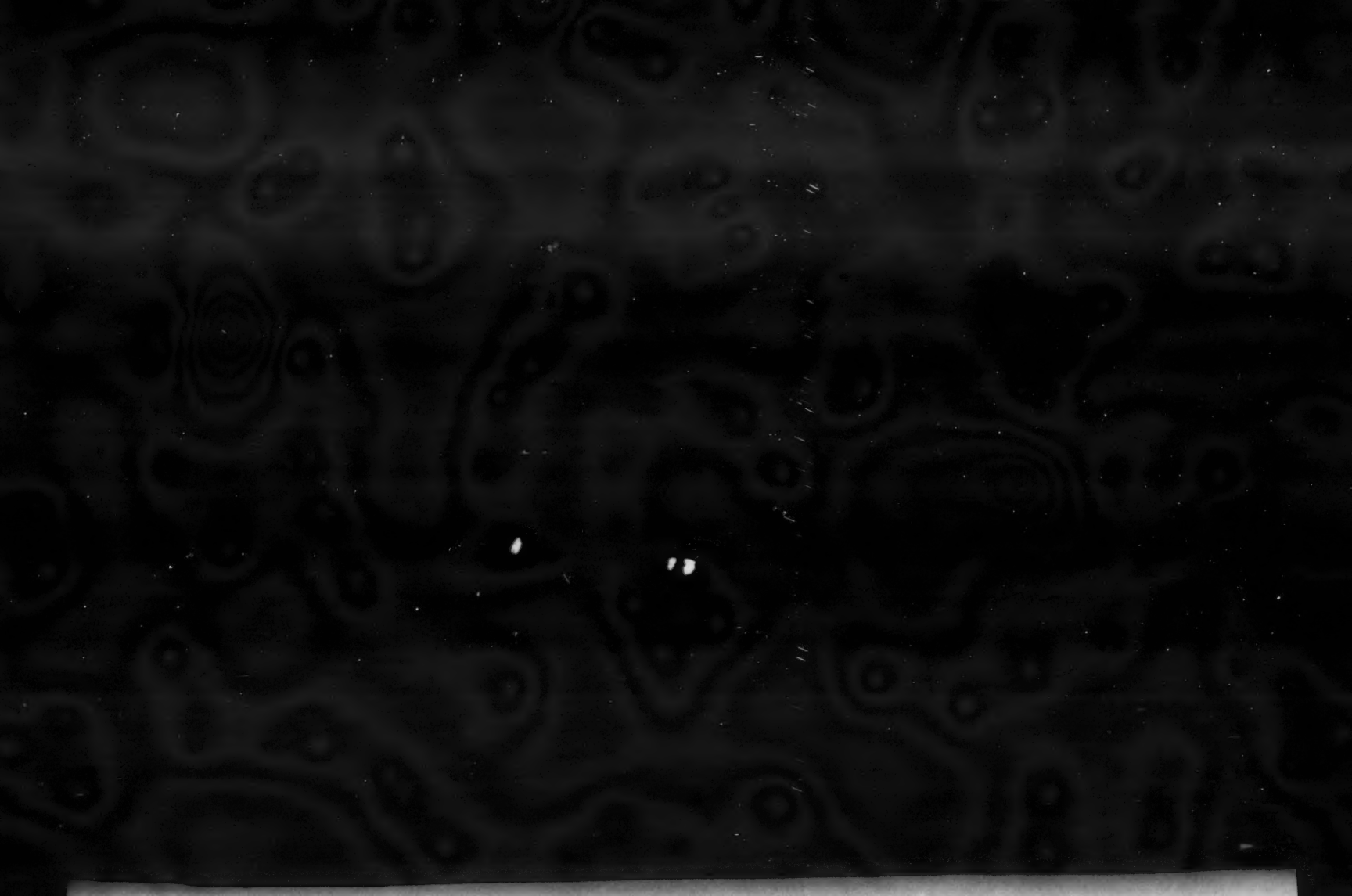
FIG. 75.—*S. cordifolia:* one sporogenous cell.

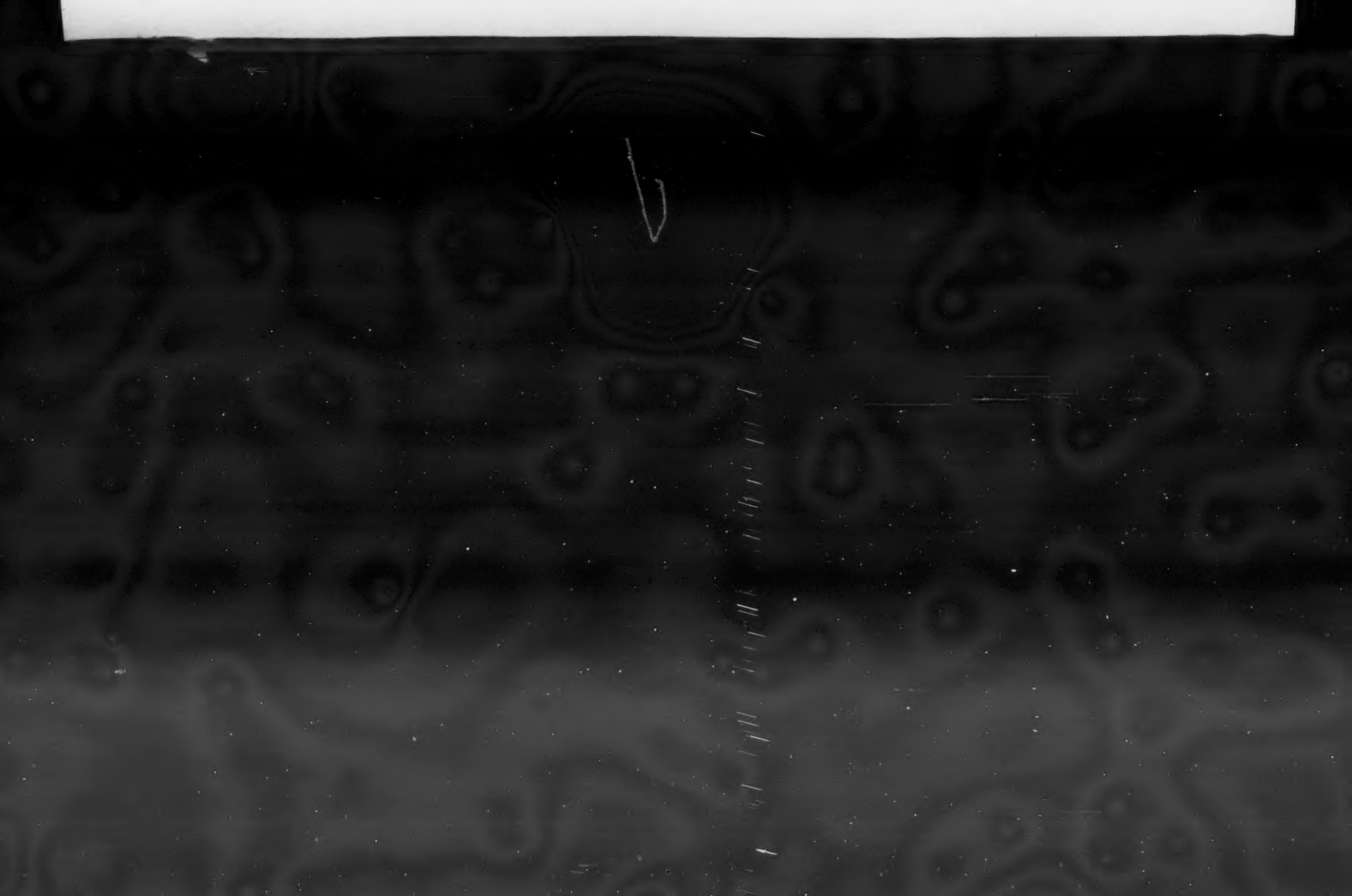
FIG. 76.—*S. crassifolia:* mother cell with three parietal cells.

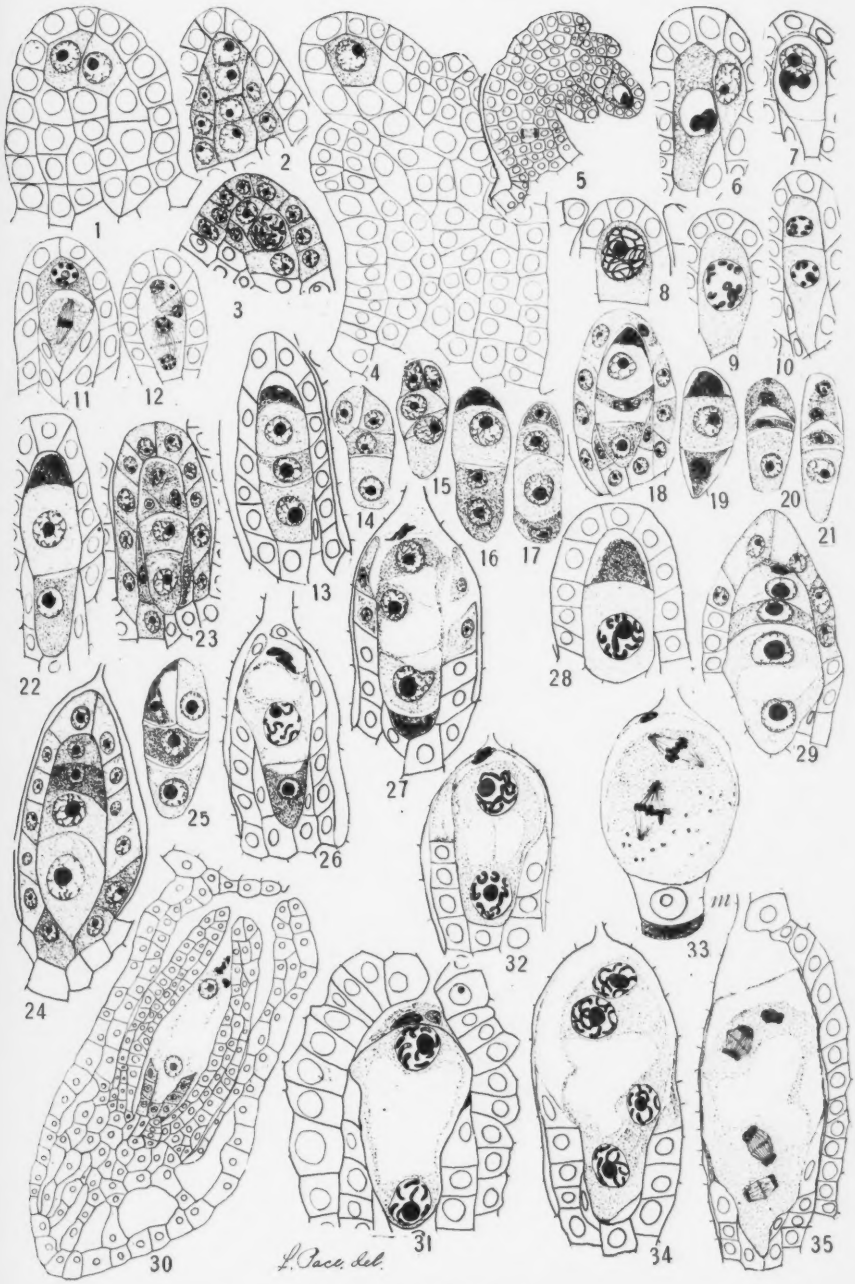
FIG. 77.—Same: entire ovule with less magnification.

FIG. 78.—*S. ligulata:* megaspores; the lower are enlarging for the embryo sac.

FIG. 79.—Same: some megaspores showing nucellar tissue above.







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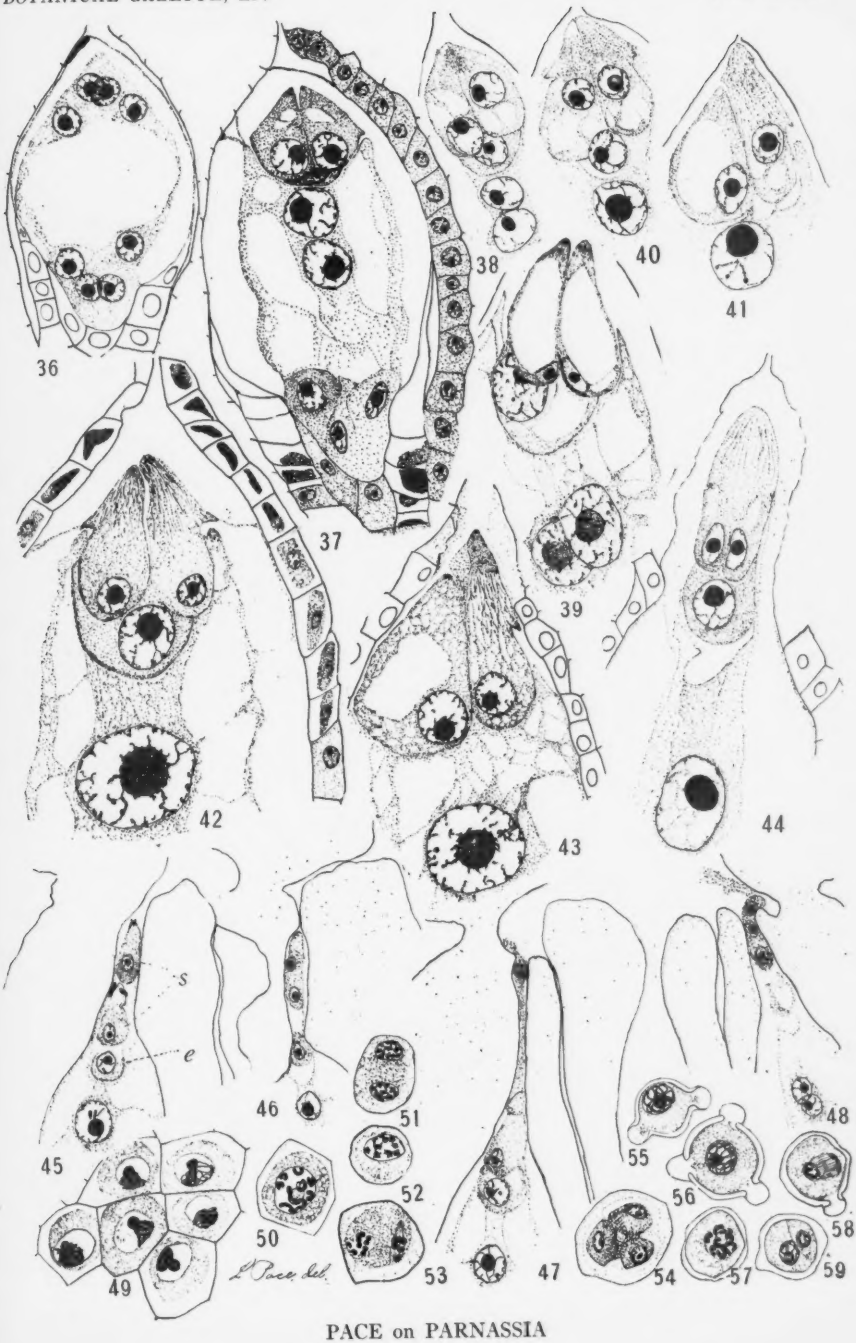

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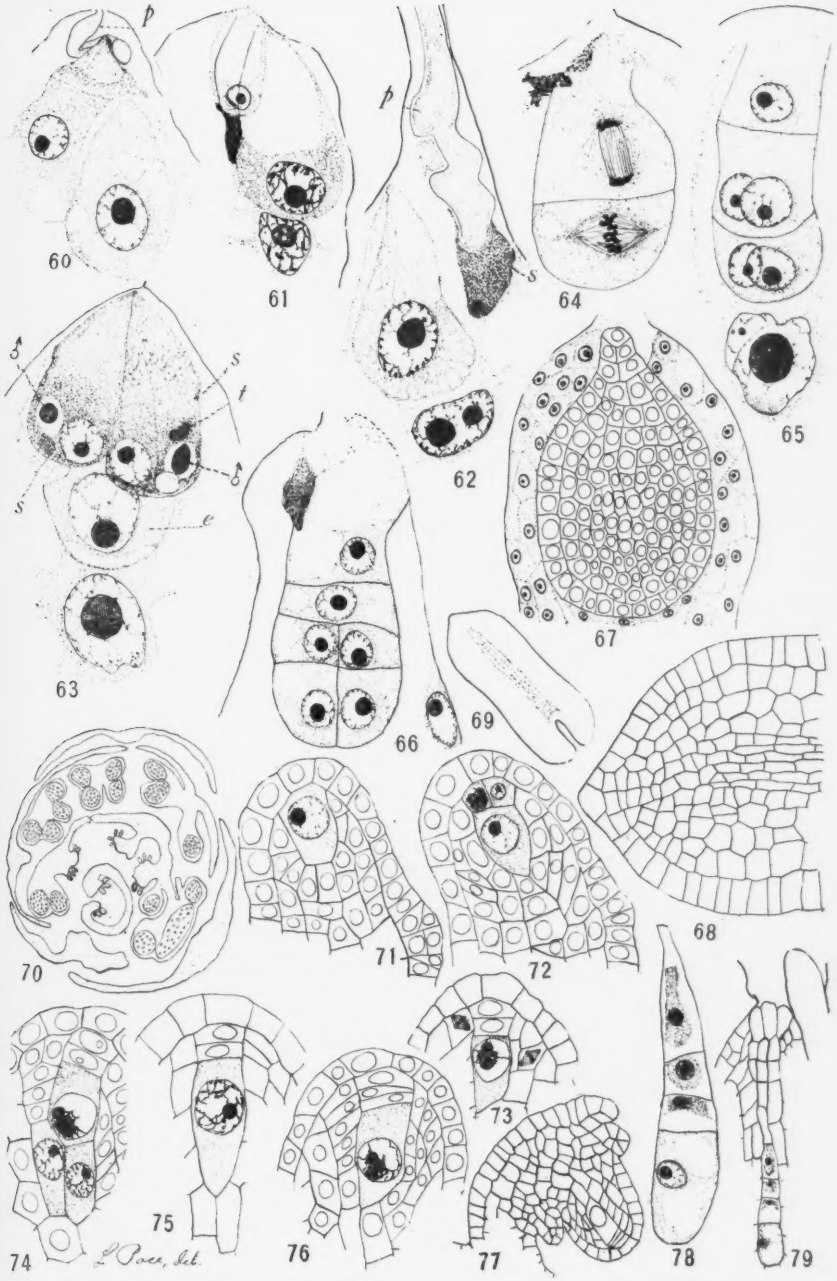

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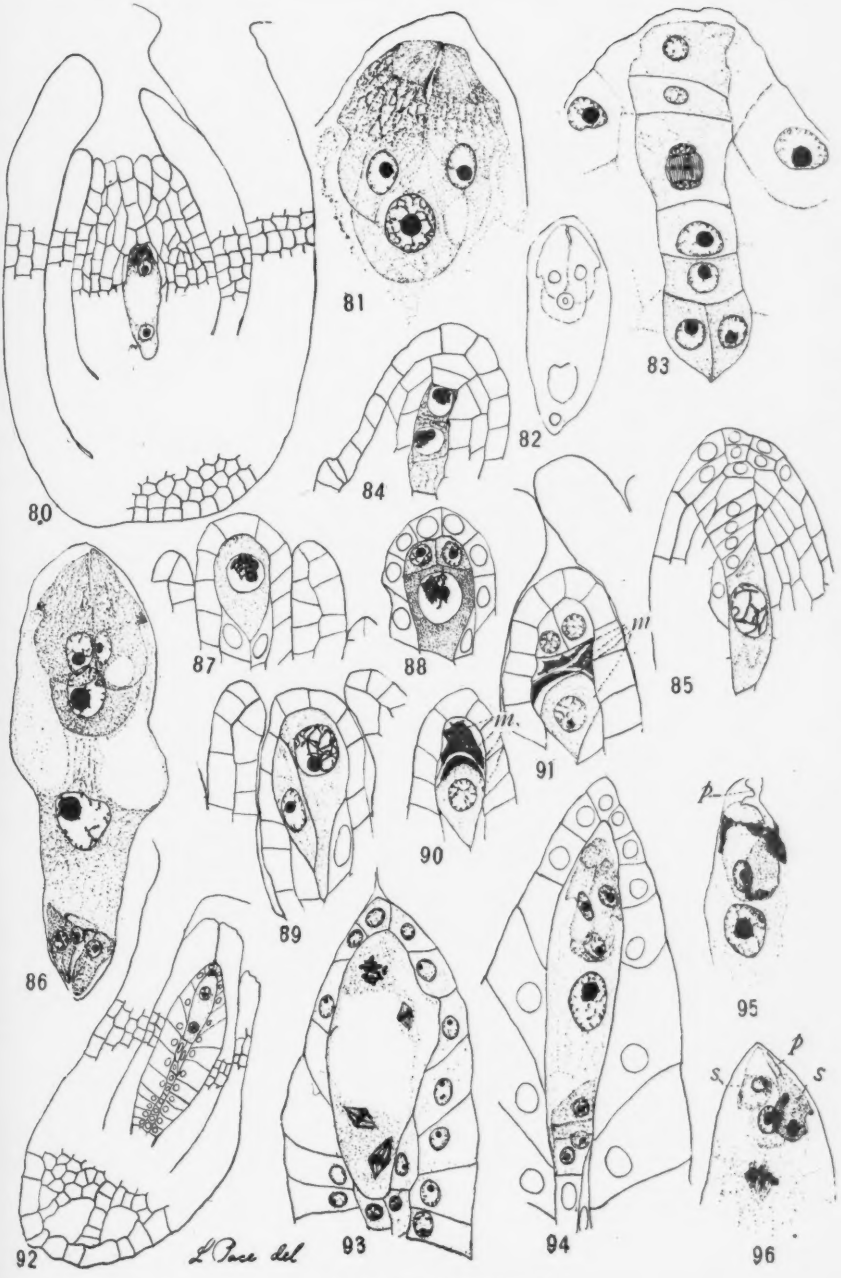

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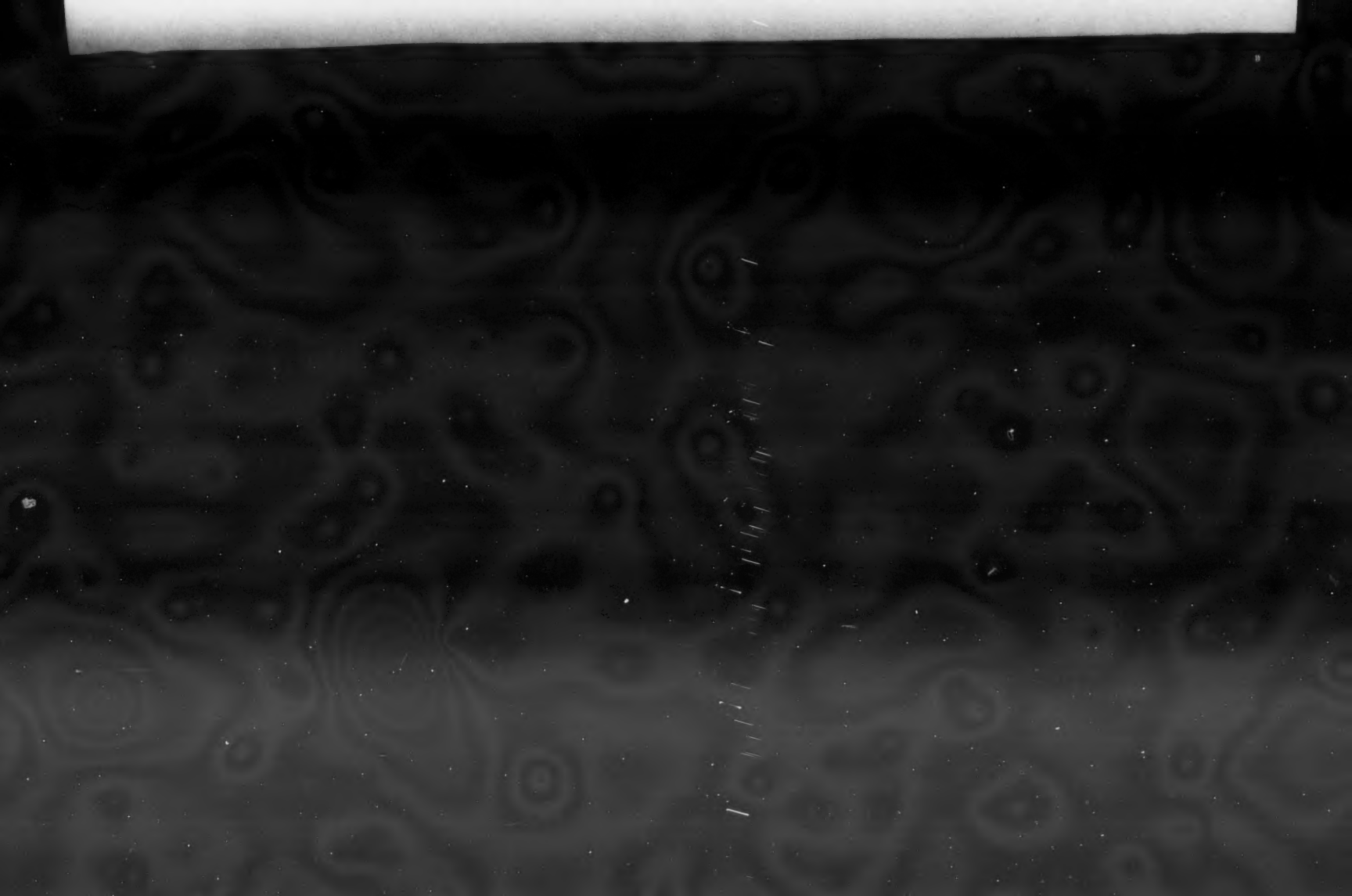


FIG. 80.—Same: a diagram of an entire ovule with two-nucleate sac; very compact tissue throughout the entire ovule.

FIG. 81.—*S. cordifolia:* egg apparatus.

FIG. 82.—Diagram of the same sac, showing one antipodal and the polars already fused near the base of the sac.

FIG. 83.—*S. crassifolia:* embryo and two endosperm nuclei.

Heuchera brixoides

FIG. 84.—Part of ovule showing two mother cells which are not exactly parallel and overlap slightly.

FIG. 85.—Mother cell after synapsis and deep in nucellar tissue.

FIG. 86.—Mature embryo sac; filiform apparatus and notch well developed in the synergids.

Drosera rotundifolia

FIG. 87.—Mother cell.

FIG. 88.—Mother cell with two hypodermal cells above.

FIG. 89.—At least two sporogenous cells, one of which has passed the synapsis stage.

FIG. 90.—Megaspores developed from a mother cell like that in fig. 87; the fourth megaspore has begun to develop the embryo sac, the other three are almost completely disorganized.

FIG. 91.—Similar megaspores, but developed from a mother cell like that in fig. 88.

FIG. 92.—An ovule with two-nucleate embryo sac; large air spaces and much spongy tissue in the lower part of the ovule; nucellar tissue with very small cells in center and very large ones next to the integument except just over the sac.

FIG. 93.—The third division in the embryo sac; in the upper nucleus the 10 chromosomes may be counted; the small nucellar cells just over the sac and the very large ones toward the base and the small ones in the center of the nucellus below the sac give the *Drosera* nucellus a very unusual appearance.

FIG. 94.—Mature embryo sac; the synergids have a well developed notch and a somewhat dome-shaped filiform apparatus; the polars have already fused.

FIG. 95.—An embryo sac with pollen tube passing around the filiform apparatus and apparently emptying into the synergid; probably the sex nuclei have already fused, but the mass is so indistinct one cannot be sure of the contents of the synergid region.

FIG. 96.—One synergid shows still a trace of the nucleus and the filiform apparatus; the other synergid shows the notch and above a bit of the pollen tube; in the lower part are two nuclei, probably the synergid nucleus and tube nucleus; the sex nuclei have fused and the endosperm nucleus is in mitosis.

DEVELOPMENT OF THE MICROSPORANGIA AND MICROSPORES OF ABUTILON THEOPHRASTI

V. LANTIS

(WITH TWELVE FIGURES)

The material used in this study was collected during September and October 1910. While many killing and fixing fluids were tried, Flemming's weaker solution proved the most satisfactory and was therefore the most generally used.

Because of the excessive development of sclerenchymatous tissue in this form, much difficulty was first experienced in sectioning. This was obviated, however, by infiltrating and imbedding in JOHNSTON'S paraffin-asphalt-rubber mixture (**11, 16**), which consists of 99 parts of paraffin (desired grade) in which has been melted enough asphalt (mineral rubber) to give the paraffin an amber color, and one part of crude india rubber. This method, in that it has proved so satisfactory, deserves a more general use among botanists. Many stains were tried, but Heidenheim's iron-alum hematoxylin, with orange G as a contrast stain, gave the best results.

The stamens of *Abutilon Theophrasti* Medic. are epipetalous, monadalphous, and branching. Occasionally the branches of the filaments are so short that the two anthers set back to back, and the two might be taken for one anther in a hasty examination. In longitudinal section the anthers are more or less crescentic in form, while a cross-section shows them to be two-rowed (fig. 5). In this respect it is very much like *Althaea rosea* Cav. (**2, 4**) and *Tilia ulmifolia* (**7**). It is not at all uncommon to see one lobe much longer and more crescentic than the other. The filament is attached to the middle of the inner side of the crescent-shaped anther. Dehiscence takes place by means of one longitudinal fissure.

There are two crescent-shaped microsporangia in each anther, one in each of the two lobes. With respect to the number of

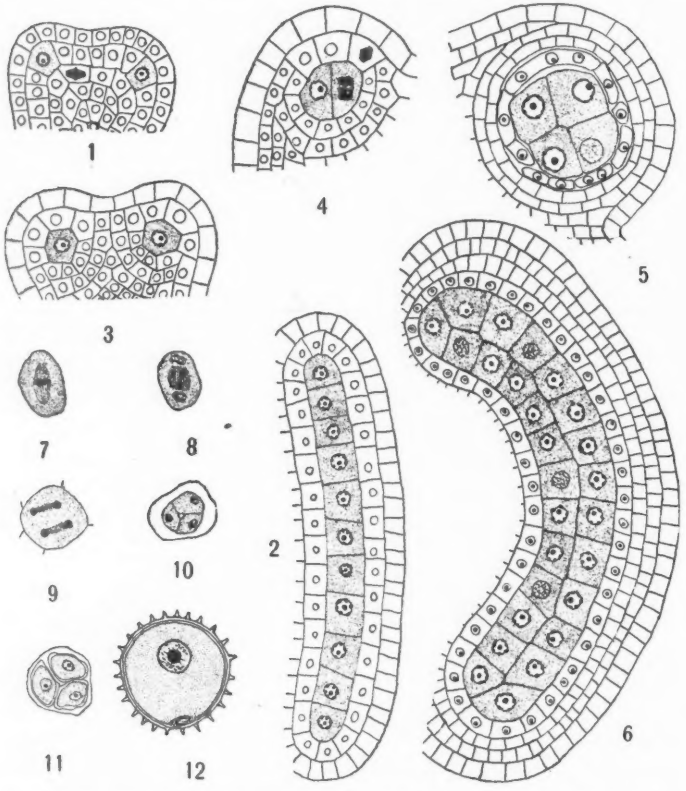
microsporangia in an anther, *Abutilon* resembles *Althaea* (**2, 4**), *Hamamelis* (**13**), *Elodea* (**12**), the Asclepiadaceae, etc.

In cross-section the archesporium is a single hypodermal cell (fig. 1). An apparent exception to this was observed in a few cases where two or three hypodermal cells, because of their size and reaction to stains, might be considered archesporial in their possibilities. The subsequent history of the anther, however, shows that there is only one true archesporial cell as seen in cross-section. While a longitudinal section of the archesporium was not observed, it is very evident that it consists of a single row of several cells, since such a section shows the primary parietal and primary sporogenous cells lying in single rows the full length of the anther (fig. 2). This condition in *Abutilon* agrees with that reported for the Malvaceae and most Compositae, and also for *Gaura* (**14**). The archesporial cells divide, as usual, by periclinal walls to form the primary parietal and primary sporogenous cells (fig. 3).

The primary sporogenous cells initiate two successive divisions, one radial and the other periclinal (figs. 4 and 5). Each primary sporogenous cell, therefore, as a rule produces only four mother cells, these four cells being almost regularly shown in a cross-section of the microsporangium (fig. 5). Thus there is quite a contrast between *Abutilon* and *Althaea rosea* (**2**), since in the latter only a single mother cell is usually to be found in a cross-section of the microsporangium, and in *Malva* also the mother cell is reported to develop directly from the primary sporogenous cell.

As may be seen from fig. 4, there are usually two parietal layers in the stage immediately preceding the formation of the mother cells. Fig. 5 shows the spore mother cell just previous to the tetrad formation. At this stage there are three parietal layers including the tapetum, which is well developed. In its origin the tapetum is like that of *Asclepias Cornuti* (**10**), *Silphium* (**9**), and other forms; and the same account is evidently true for *Althaea*, as may be judged from SACHS'S figure (**2**, fig. 377). The tapetum reaches its highest development about the time of the tetrad formation, as is true in most angiosperms. Its development is much later than that of the tapetum of *Euphorbia* (**8**).

At about the time the mother cells are dividing or a little earlier, the nuclei of some of the tapetal cells divide without the formation of cell walls, and tapetal cells with one, two, or three nuclei are found, being much like those described for *Hamamelis* (13), *Ipomoea purpurea* (19), and *Ulmus* (15) in this respect.



FIGS. 1–12.—Fig. 1, cross-section of the anther showing archesporium; fig. 2, primary sporogenous and primary parietal cells in longitudinal section; fig. 3, primary sporogenous cell and plate of parietal cells in cross-section; fig. 4, two daughter cells of primary sporogenous cell in cross-section; fig. 5, cross-section of spore mother cells; fig. 6, longitudinal section of spore mother cells; fig. 7, first division of spore mother cell; fig. 8, two-celled stage of spore mother cell; fig. 9, second division of spore mother cell; fig. 10, tetrad, early stage; fig. 11, later stage of tetrad; fig. 12, mature pollen grain.

The tapetal cells having two or three nuclei are generally more or less elongated (fig. 5).

The spore mother cell is a much prolonged stage, and the second reduction division follows very closely after the first, no walls being formed until after the four nuclei have appeared (figs. 8 and 9), a condition characteristic of the dicotyledons. The tetrad is tetrahedral in arrangement (figs. 10 and 11), no exceptions being observed.

Special study was not made of the composition of the wall of the developing microspores, but evidently it is similar to the microspore walls of *Althaea* (**6**), *Malva* (**5**), and *Ipomoea* (**19**). Since the tapetum reached its highest development during the formation of the tetrad, the mother cells do not become isolated early, but remain intact as in *Althaea* (**1, 2**). While the spore walls are being formed, the tapetum begins to disorganize, but does not entirely disappear until the pollen grains are practically mature. In this respect *Abutilon* resembles *Oenothera* (**17**), *Gaura Lindheimeri* (**14**), etc.

The mature pollen grain is spherical, has both intine and exine well developed, and is covered with spines (fig. 12). Only two nuclei, the tube nucleus and the generative nucleus, were found in the mature pollen grain.

Summary

Abutilon Theophrasti shows the single row of archesporial cells that has been reported for the other two investigated species of Malvaceae, and in the formation of primary parietal and primary sporogenous layers there is also great similarity.

In *Abutilon*, however, each primary sporogenous cell produces four mother cells, while in the other Malvaceae studied only one is formed.

The mother cell stage in *Abutilon* persists until three parietal layers, the inner being a well developed tapetum, are fully formed, after which the characteristic heterotypic and homotypic divisions take place rapidly.

This period of tetrad formation is marked by a multiplication of nuclei in the tapetal cells.

The arrangement of the microspores in the tetrad is tetrahedral and very regular. The tapetum continues to inclose the microspores until they develop their own cell walls and the wall of the mother cell disorganizes, when the tapetal cells gradually disappear. This long persistence of the tapetum is also true of *Althaea rosea*.

The spherical pollen grain of *Abutilon* agrees with that of other described Malvaceae in the number of nuclei and the structure and composition of the walls.

This work has been done in the Botanical Laboratory of the University of Cincinnati, under the direction of Professor H. M. BENEDICT, whom the writer wishes to thank for suggestions and criticisms. Much of the literature was reviewed at the Lloyd Library of Cincinnati, and the writer desires to acknowledge favors received from Mr. WM. HOLDEN, the librarian.

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BRIEFER ARTICLES

ARTIFICIAL PRODUCTION OF ALEURONE GRAINS

(WITH ONE FIGURE)

As is well known, aleurone grains consist mainly of protein material which may be wholly amorphous or partly amorphous and partly crystalline. In the latter case each grain consists typically of a crystal of protein (crystalloid), and an envelope of amorphous protein material whose outer layer may be differentiated from the rest. There is usually included in the envelope a globule of mineral matter or organic material combined with mineral matter (globoid). The variations occurring in different plants have been fully described by PFEFFER.[1]

Each grain is laid down in a vacuole in the protoplasm through the activity of the protoplasm itself. Its manufacture is therefore a distinctly vital process. It is the object of this paper to show that bodies of the same structure may be produced artificially. The resemblance is so striking as to leave little doubt that the essential features of the natural process have been successfully imitated.

The first step in the procedure is the preparation of protein according to the following method of OSBORNE.[2] Half a pound of *Bertholletia* nuts, after the shells have been removed, are ground into a pulp. The fatty material is then removed by repeated thorough treatments with ether, the small portion of the solvent which remains in the solid after the final decantation being allowed to evaporate completely. To the dry residue is added four or five times its volume of 10 per cent NaCl solution in which it stands some hours. Frequent shaking accelerates the dissolving of the protein. The solution of protein is then decanted and thoroughly filtered. At first the finer particles come through, but on repeated filtering through the same paper there results an absolutely clear liquid which microscopic examination shows to be without particles of any kind. This clear filtrate is placed in a dialyzer, and after some hours the sodium chloride is sufficiently removed to cause the precipitation of the protein.

Most of the protein is precipitated as clear, well formed crystals of the hexagonal system. Their thickness is usually about one-sixth

[1] PFEFFER, W., Jahrb. Wiss. Bot. **8**: 429. 1872.

[2] OSBORNE, T. B., Amer. Chem. Jour. **14**: 622. 1892.

of their width. Truncated crystals are common, especially those in which one side is about half as long as the opposite side.

Among the naked crystals are others which are furnished with an envelope (fig. 1, *a*, *b*, *g*); the whole then resembles an aleurone grain. The inclosed crystals may resemble any of the free forms, but are usually complete hexagonal crystals. They may also be of various sizes, but are usually about the size of the natural aleurone grain. Rarely more than one enters into the composition of a single grain (fig. 1, *h*), as happens also in some kinds of natural grains.

The envelope varies in thickness independently of the size of the crystal. It is usually arranged symmetrically about the latter, but the truncated crystals have a tendency to occur at one side. The outline of the grain is then globular or slightly elliptical, but not angular. Occasionally the outermost layer of the envelope differs from the rest in being more opaque and slightly granular (fig. 1, *g*), when it takes the form of a narrow but distinct membrane. This resembles the similar structure sometimes found in natural aleurone grains.

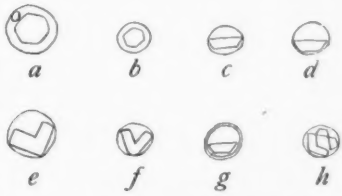

FIG. 1.—Artificial aleurone grains: *a*, protein crystal surrounded by an amorphous protein envelope in which is included a drop of oil which in size and position resembles a globoid; *b*, similar body without an oil drop; *c–h*, various forms of crystals resembling those which occur in natural aleurone grains; *g*, the amorphous envelope with a differentiated outer layer such as occurs in some natural grains; *h*, grain containing three crystals, a condition sometimes found in natural grains.

In an experiment in which some fatty matter had not been removed by the ether, many extremely small oil droplets came through the filter and were deposited with the artificial grains. A small number of these had been incorporated into the grains, each of which then consisted of a crystal, an oil droplet, and an envelope. The oil droplet thus resembled the globoid of the natural aleurone grain and the whole artificial grain was extremely similar in appearance to the natural one. In view of this it seems very probable that artificial globoids could easily be produced as inclusions in the artificial aleurone grains by causing dissolved globoid material to precipitate during the formation of the protein crystals. But this did not seem to be sufficiently important to warrant any special effort directed to this end, particularly as globoids do not always accompany the crystals in natural aleurone grains.

The yield of artificial grains varies exceedingly in different experiments. Though two experiments may be performed apparently in exactly the same manner, the number of grains obtained may be vastly different; indeed in some experiments scarcely any are produced. As a rule the first solution extracted from any given preparation gives the best results.

Chemical tests show that the grains are composed of protein, for they respond strongly to all the protein tests such as the xanthoproteic, Millon's, etc. In each test the envelope responded just as strongly as the crystal; it consists, therefore, of uncrystallized protein. With other chemical reagents their behavior is that which is to be expected; they are insoluble in water, alcohol, and sodium carbonate, soluble in weak acids and alkalies and in salt solutions. No marked difference could be observed between the solubility of the envelope and that of the crystal.

Under the action of putrefying bacteria, however, the behavior of the envelope and crystal is occasionally different. In some cases the crystal was dissolved out, leaving the ruptured envelope free; the latter then became flattened out or turned back at the edges.

In the presence of a disinfectant to prevent putrefaction, the grains usually remain unchanged indefinitely. Sometimes, however, the envelope becomes more or less angular, the angles corresponding to those of the crystal.

The proteids of other seeds were used in these experiments, but in no case could artificial grains be obtained. Castor bean, hemp, and lupine gave only crystals without envelopes.

In the case of *Bertholletia*, however, it seems evident that structures resembling the aleurone grains formed through the activity of the protoplasm have been produced in the laboratory. This imitation consists not only in reproducing what is probably the same chemical compound, but also in reproducing the same morphological structure.

In conclusion I wish to acknowledge my indebtedness to Professor W. J. V. Osterhout, in whose course in plant physiology the original observation was made, and with whose advice the subsequent work was done.—W. P. Thompson, *Harvard University*.

CURRENT LITERATURE

NOTES FOR STUDENTS

Metabolism of fungi.—Recently a number of papers on the metabolism of fungi have appeared, which, although they represent various phases of the subject, may be noted here in a collective review. Since PASTEUR's discovery of the biological method for separating stereoisomeric components from their racemic compounds, the study of the action of fungi on compounds having asymetric carbon atoms has been of great interest. The work of the earlier investigators, like that of LE BELL, LEUKOWITSCH, SCHULZE and BOSSHARD, and others, was concerned chiefly with the chemical aspects of the subject, with the purpose of resolving racemic compounds into their optically active components.

Taking up the subject more in its biological aspect, for the purpose of determining whether any fungi are able to utilize both components of racemic compounds to an equal extent, PRINGSHEIM[1] has investigated the action of 16 fungi and 2 bacteria on leucine and glutaminic acid, from which SCHULZE and BOSSHARD[2] had obtained *d*-leucine and *l*-glutaminic acid by the action of *Penicillium*. PRINGSHEIM found that in all cases both of the components of the amino-acids used were partly consumed by the organisms. In about one-half of the experiments both components were consumed to an equal degree, so that the recovered portions of the acids were optically inactive. In the remaining instances one isomer was consumed to a greater extent than the other, the naturally occurring component being the one consumed most readily in all such cases.

HERZOG and his students have taken up the study of the action of fungi on *d-l*-oxyacids and *d-l*-amino-acids in order to gain a knowledge of the process involved in the utilization of one of the isomers of the inactive forms of these acids. The experimentation was carried out both with living fungi and with mycelia killed by various means. In the experiments with living material the fungi were grown in flasks of suitable culture media until the carbon dioxide production became constant. A definite quantity of the acid to be tested was then introduced into the flasks and the subsequent carbon dioxide output determined. At the end of the experiment the residual acid was

[1] PRINGSHEIM, HANS, Studien über Spaltung racemischer Aminosäuren durch Pilze. Zeitschr. Physiol. Chem. **65**:96–109. 1910.

[2] SCHULZE, E., und BOSSHARD, E., Untersuchungen über die Aminosäuren welche bei der Zersetzung der Eiweissstoffe durch Salzsäure und durch Barytwasser entstehen. II. Zeitschr. Physiol. Chem. **10**:134–145. 1886.

determined and its rotation measured. In the experiments with fungi killed by acetone, methyl alcohol, or other means, the powdered fungus material was added to flasks containing solutions of the acids. The carbon dioxide products and residual acid were determined as before.

In the first experiments reported by HERZOG and MEIER[3] it was found that the addition of lactic, tartaric, malic, mandelic, and β-oxybutyric acids to cultures of *Penicillium glaucum*, in which the carbon dioxide production had become fairly constant, resulted in a great increase of the carbon dioxide output. In every case the excess of carbon dioxide over the normal was much greater than that calculated on the assumption that all of the acid used up had been completely oxidized to carbon dioxide and water. Under the same conditions glycollic, citric, pyrotartaric, and oxybutyric acids gave no increase in the carbon dioxide production. The authors suggest that these experiments indicate that the biological splitting of substances containing an asymmetric carbon atom depends on a process of oxidation. Only the acids having an asymmetric carbon atom were oxidized.

To test this hypothesis further, experiments were carried out with fungous material killed with acetone and methyl alcohol and finely pulverized. Definite quantities of the material were added to flasks containing solutions of lactic acid or sodium lactate, and also to control flasks containing distilled water. It was found that the carbon dioxide production in the flasks containing the acid or its salt was slightly greater than in the controls.

In a second paper[4] the method of experimentation with killed mycelia is applied to the study of a number of other acids. The mycelia in these experiments were immersed in liquid air, by which, it was assumed, the cells were killed, although the spores were subsequently found to be alive. In these experiments it was found that *d*-tartaric acid, *l*-tartaric acid, and *d-l*-tartaric acid were oxidized, while mesotartaric acid, which is not separable into optically active components, was left intact. The dextro-rotatory form was oxidized most rapidly. The optically active isomers of lactic acid showed scarcely any difference in the rate of oxidation, while *l*-mandelic acid was oxidized more rapidly than its antipode. Glycollic acid, having no asymmetric carbon atom, was not attacked. The authors conclude that the preferential oxidation of one component of a racemic mixture, which has heretofore been regarded as biological selections of food substances, is merely the result of differences in the reaction velocities of the antipodes with the substances of the organisms.

In continuation of the foregoing work, HERZOG and RIPKE[5] have studied

[3] HERZOG, R. O., und MEIER, A., Ueber Oxydation durch Schimmelpilze. Zeitschr. Physiol. Chem. **57**: 35–42. 1908; also MEIER, A., Dissertation under the same title. Karlsruhe. 1909.

[4] ———. *Ibid.* **59**: 57–62. 1909.

[5] HERZOG, R. O., und RIPKE, O., Ueber das Verhalten einger Pilze zu organischen Säuren. *Ibid.* **73**: 284–289. 1911.

the effects of *Oidium lactis* killed with acetone and ether on the lactic, succinic, and mandelic acids. The results obtained do not conform with those obtained in the foregoing experiments with *Penicillium*. Only lactic acid gave a greater carbon dioxide production than the control with distilled water. With mandelic and succinic acids the control flasks yielded greater amounts of carbon dioxide. In an experiment in which the fungus was left in liquid air for several hours, subsequent cultures showed that the cells had not all been killed.

A similar set of experiments carried out by HERZOG, RIPKE, and SALADIN[6] with acetone preparations of *Mycoderma cerevisiae* showed that with acetic acid and lactic acid the carbon dioxide production was less in the acid medium than in distilled water, although a part of the acid in each case had disappeared. The carbon dioxide output in experiments with the different isomeric modifications of mandelic and tartaric acids was not determined, but the whole added quantity of these acids could not be recovered. In some cases with mandelic acid the total acid content of the controls at the end of the experiment was as great as that in flasks to which acid had been added. The authors assume that the autolytic production of acid by the killed fungus cells reaches a certain maximum. If that maximum has been attained by the addition of a foreign acid, no further spontaneous acid formation occurs. Succinic acid depressed the production of carbon dioxide, but there was no evidence that any of the acid had disappeared. The general conclusion from this last set of experiments is that the production of carbon dioxide by killed cells of *Mycoderma* is depressed in acid media, although the quantity of acid is diminished. The disappearance of the acid, therefore, cannot be explained as a process of oxidation, nor is the process one of metabolism, since the cells were dead. In view of the comparatively small quantities of acids which disappeared apparently through the action of the killed fungus cells, the experiments would have been more convincing if the authors had reported control experiments showing how much of the acids could be immediately recovered from the mixtures.

In another paper by HERZOG and SALADIN[7] the effect of leucine on the carbon dioxide production of *Penicillium* is reported. The method of experimentation was similar to that described above in the experiments of HERZOG and MEIER, and the results were comparable to those obtained with oxyacids. The addition of leucine was followed by an increased production of carbon dioxide, which was greater than that calculated on the assumption that all the available leucine had been oxidized to carbon dioxide and water.

The important series of researches of EHRLICH[8] on the behavior of amino-

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[6] HERZOG, R. O., RIPKE, O., und SALADIN, O. *Ibid.* **73**: 290–301. 1911.

[7] HERZOG, R. O., und SALADIN, O., Ueber das Verhalten einiger Pilze gegen Aminosäuren. *Ibid.* **73**: 302–307. 1911.

[8] For a general account of this work see EHRLICH, F., Ueber die chemischen Vorgänge pflanzlichen Erweissstoffwechsels und ihre Bedeutung für die Alkoholische Gärung und andere pflanzenphysiologische Processe. Landwirth. Jahrb. **38**: 289–327. 1909.

acids in alcoholic fermentation has greatly advanced our knowledge of the origin of fusel-oils, which have usually been regarded as side-products of sugar fermentation. These investigations have been extended by EHRLICH and JACOBSON[9] to other fungi, to determine whether the decomposition of amino-acids induced by them is similar to that brought about by the yeast cell. The authors have studied the action, on amino-acids, of some 50 fungi, upon which a complete report is promised. The behavior of the filamentous fungi toward amino-acids differs greatly according to whether carbohydrates are present or not. In the absence of carbohydrates the decomposition of amino-acids is more extensive than that produced by yeasts, but in the presence of carbohydrates the degree of decomposition differs with different fungi. In the present paper the peculiar behavior of *Oidium lactis* on amino-acids in the presence of sugar is reported. The action of this fungus results in the replacement of the amino-groups by hydroxyl, thereby yielding oxyacids corresponding to the amino-acids according to the following general reaction:

$$R \cdot CH(NH_2)CO_2H + H_2O = R \cdot CH(OH)CO_2H + NH_3$$

The ammonia which is formed is used in protein synthesis by the fungus. Here as with the yeast cell the amino-nitrogen (in the form of ammonia) enters into the metabolism of the cell, while the rest of the molecule is excreted as a product not capable of being further utilized. The end products in the two cases are different, being in the case of the yeast cell an alcohol with one carbon less than the amino-acid from which it was derived, while with *Oidium lactis* an oxyacid corresponding to the amino-acid results. By the action of *Oidium lactis*, *l*-tyrosin yielded *d*-paraoxyphenyl-lactic acid, *d-l*-phenylalanin yielded *d*-phenyl-lactic acid, and *l*-tryptophan gave *l*-indol-lactic acid, all acids which were heretofore not known in those modifications.

In this connection the authors point out that KOTAKE[10] obtained from dogs suffering from phosphorus poisoning the levorotatory form of oxyphenyl-lactic acid, thus affording an example of the production by the plant and by the animal cell, not of the same but of opposite stereoisomers from one and the same substance. It should be stated, however, that KOTAKE himself regards it as extremely improbable that his acid was produced from tyrosin, as he was unable to isolate oxyphenyl-lactic acid as a result of feeding tyrosin itself.

A better example of the production of isomeric antipodes from the same racemic substance is afforded by the action of plant cells and of animal cells on racemic phenylamino-acetic acid. NEUBAUER and WARBURG[11] obtained the

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[9] EHRLICH, FELIX, und JACOBSON, K. A., Ueber die Umwandlung von Aminosäuren in Oxysäuren durch Schimmelpilze. Ber. Deutsch. Chem. Gesells. **44**: 888–897. 1911.

[10] KOTAKE, Y., Ueber *l*-Oxyphenylmilchsäure und ihr Vorkommen im Harn bei Phosphorvergiftung. Zeitschr. Physiol. Chem. **65**: 397–401. 1910.

[11] NEUBAUER, O., und WARBURG, O., Ueber eine Synthese mit Essigsäure in der künstlich durch bluteten Leber. *Ibid.* **70**: 1–9. 1910.

d-acetylphenylamino-acetic acid from this substance injected into the liver of dogs, while NEUBAUER and FROMHERZ[12] obtained the *l*-acetylphenylamino-acetic acid as a result of yeast fermentation of the same racemic compound.

The intermediate chemical transformations by which *d*-amino-acids are changed into alcohols with one carbon atom less in fermentation have been investigated by NEUBAUER and FROMHERZ and described in the paper cited above. The content of the paper is largely chemical. The conclusion is reached that the amino-acids are not directly transformed into alcohols by hydrolysis and subsequent splitting off of ammonia and carbon dioxide, as represented by the general formula

$$R \cdot CH \cdot NH_2 - COOH + H_2O = R \cdot CH_2OH + CO_2 + NH_3$$

but that keto-acids are first formed, and these, by loss of carbon dioxide and reduction, are changed into alcohols, the main steps of the process being represented as follows:

$$R - CHNH_2 - COOH + O = R - CO - COOH + NH_3$$
$$R - CO - COOH \rightarrow R \cdot CHO + CO_2$$
$$R - CHO + 2H = R - CH_2OH$$

This interpretation is the result of experiments in which it was shown (1) that a keto-acid (phenylglyoxylic acid) was formed by the fermentation of phenyl-amino-acetic acid, and (2) that a keto-acid (*p*-oxyphenylpyrotartaric acid) yielded the same alcohol by fermentation as the corresponding amino-acid (tyrosin).[13] A number of side reactions and secondary products occur in this process. The occurrence of the aldehyde is postulated. According to the authors the decomposition of amino-acids by yeasts is hereby shown to follow the same course as the decomposition of these acids in the animal body, except that the postulated aldehyde which is reduced to alcohol by the yeast cell is oxidized to the corresponding fatty acid which is further utilized in metabolism by the animal cell.

The discovery by EHRLICH[14] of the production of fumaric acid from sugar through the agency of *Rhizopus nigricans* is of great biological interest, not only because it is the first instance of the occurrence of fumaric acid as a product of metabolism of micro-organisms, but also because of its possible bearing on the origin of unsaturated acids in higher plants. The acid was isolated by EHRLICH from culture solutions, containing much sugar, upon which *Rhizopus nigricans* was grown. The quantity of acid varies with the sugar content, but in old cultures from which the sugar has disappeared the acid is again consumed.

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[12] NEUBAUER, O., und FROMHERZ, K., Ueber den Abbau der Aminosäuren bei der Hefegärung. Zeitschr. Physiol. Chem. **70**: 326-350. 1911.

[13] EHRLICH, FELIX, Ueber die Vergärung des Tyrosins zu *p*-Oxyphenyl-äthyl-alkohol (Tyrosol). Ber. Deutsch. Chem. Gesells. **44**: 139–146. 1911.

[14] ———, Ueber die Bildung von Fumarsäure durch Schimmelpilze. Ber. Deutsch. Chem. Gesells. **44**: 3737–3742. 1911.

With glycerin, alcohol, or peptone as sources of carbon, no fumaric acid is produced. The fact that fumaric acid here occurs as an intermediate product in the metabolism of sugar suggests that unsaturated acids in higher plants may result from carbohydrate metabolism. That a close relation exists between the higher unsaturated acids and carbohydrates in plant metabolism has been generally conceded by plant physiologists since the work of MAQUENNE.

That many fungi and bacteria are able to utilize fats has been shown by several investigators. A further contribution to the subject has been made by OHTA,[15] who studied the decomposition of the fat of horse liver caused by five forms of fungi obtained by exposing culture plates in the laboratory. The forms were *Cladosporium herbarum*, *Penicillium glaucum*, *Aspergillus glaucus*, *A. nidulans*, and *Actinomucor repens*. All of these caused the disappearance of fat from the ground sterilized liver tissue. *Actinomucor* was the most active, causing the disappearance of over 60 per cent of the fat in three weeks. Of the others, *Aspergillus* used 17–20 per cent, *Cladosporium* 14 per cent, and *Penicillium* 6–8 per cent. Attempts to grow *Actinomucor* on culture solutions containing fat as the only source of carbon, in order to study the mode of decomposition of the fat, were unsuccessful. The paper contains detailed notes on the methods and precautions to be observed in making fat determinations in work of this kind.

Another contribution to the subject of the utilization of fat by fungi has been made by ROUSSY,[16] who experimented with the following forms: *Absidia glauca*, *Circinella umbellata*, *Mucor mucedo*, *Phycomyces nitens*, *Rhizopus nigricans*, *Sporodinia grandis*, *Morteirella candelabrum*, *Aspergillus flavus*, *Citromyces glaber*, *Penicillium luteum*, *Sterigmatocystis nigra*, and *Sporotrichum bombyceum*. All of these grew well on fats and oils of various kinds. To determine if it was the fatty acid or the glycerine which was utilized, cultures were made in Raulins solution in combination with oleic, palmitic, or stearic acid or glycerine. It was found that the fungi thrived well on the fatty acids, but only *Aspergillus* and *Penicillium* grew on glycerin solutions.

REICHEL, studying the effects of acetic acid and its salts on a form of *Penicillium*, has rediscovered the fact that the toxicity of that acid is mainly due to the action of the undissociated molecule. He finds that acetic acid is poisonous in much lower concentrations than those at which the strong mineral acids are toxic, but, owing to its slight dissociation, its toxicity cannot be attributed to the hydrogen ion. At the same time, the salts of acetic acid, which are highly dissociated, are not poisonous, hence the acetate ion is not poisonous. The toxicity of acetic acid, therefore, must be attributed to the molecule as a whole.

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[15] OHTA, KOHSHI, Ueber die fettzehrenden Wirkungen der Schimmelpilze nebst dem Verhalten des Organfettes gegen Fäulniss. Biochem. Zeitschr. **31**: 177–194. 1911.

[16] ROUSSY, A., Sur la vie des Champignons dans les acides gras. Compt. Rend. **153**: 884–886. 1911.

The same conclusion reached by CLARK[17] by similar experimentation and reasoning many years ago seems to have escaped his notice.

REICHEL[18] further points out that the addition of mineral acids to solutions containing acetates produces the same effect as the addition of acetic acid, since the acetic acid is replaced in its salts by the stronger acids and undissociated acid is formed in the solution as a result of the establishment of a new equilibrium. In solutions whose acidity is not great enough to inhibit growth entirely, the author finds a certain regulatory depression of the acidity by the fungus until more favorable concentrations are attained. This phase of the subject seems to demand further investigation to determine whether such purposeful regulation really exists. Under certain conditions, at any rate, depending upon the substances available in the medium, either acid or alkali will accumulate in culture solutions through the action of fungi to such a degree as to inhibit growth entirely.[19]

BORKORNY[20] reports a number of miscellaneous experiments and observations indicating that methyl alcohol can be used as a source of carbon by some fungi and bacteria. A yeast not capable of fermenting cane sugar or glucose grew spontaneously on a solution of mineral nutrients to which 0.1 per cent of methyl alcohol had been added. Inoculations from this culture were made in solutions containing 0.0025 per cent to 5 per cent methyl alcohol. After a time the flasks contained vegetations of yeast and bacteria and in some cases infusoria were present. Apparently no precautions were taken to avoid contamination, so that it is possible that carbon compounds were introduced in the form of dust particles.

SAITO[21] reports the formation of lactic acid by *Rhizopus chinensis*, thus confirming the observations of EIJKMAN and of CHRZASZCZ, who reported the production of lactic acid by *Rhizopus Rouxii*. These observations had been doubted because other instances of the production of lactic acid by filamentous fungi are not known. SAITO identified his acid by means of the zinc and the calcium salts and by the reaction of UFFELMAN.

GOUPIL[22] finds that *Rhizopus Rouxii* produces in cultures up to 4 grams

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[17] CLARK, J. F., On the toxic effect of deleterious agents on the germination and development of certain filamentous fungi. BOT. GAZ. **28**: 289–327; 378–404. 1899.

[18] REICHEL, J., Ueber das Verhalten von *Penicillium* gegenüber der Essigsäure und ihren Salzen. Biochem. Zeitschr. **30**: 152–159. 1910.

[19] HASSELBRING, H., The carbon assimilation of *Penicillium*. BOT. GAZ. **45**: 176–193. 1908.

[20] BORKORNY, TH., Beobachtungen über Pilze, welche Methylalkohol als C-Quelle verwenden können. Centralbl. Bkt. II. **29**: 176–188. 1911.

[21] SAITO, K., Ein Beispiel von Milchsäurebildung durch Schimmelpilze. Centralbl. Bakt. II. **29**: 289–290. 1911.

[22] GOUPIL, R., Recherches sur *l'Amylomyces Rouxii*. Compt. Rend. **153**: 1172–1174. 1911.

per liter of succinic acid mixed with some acetic and some butyric acid. Contrary to the statements of some workers, oxalic and lactic acids are not produced. He believes that the succinic acid is formed from sugar and not from any amino-acid.—H. HASSELBRING.

Current taxonomic literature.—G. E. OSTERHOUT (Muhlenbergia **8**:44, 45. 1912) characterizes a new *Cogswellia* (*C. concinna*) and a new variety of *Gnaphalium* (*G. decurrens* var. *glandulosum*) from Colorado.—Q. PAULSEN (Arb. Bot. Have Kb. no. 65. 303–318. 1911) under the title "Marine plankton from the East-Greenland Sea" records the Peridiniales found on the Danish Expedition to Greenland in 1906–1908 and describes a new species of *Peridinium* (*P. varicans*), also a new species doubtfully referred to *Apodinium*.—W. H. RANKIN (Phytopathology **2**:28–31. *pl. 3.* 1912) describes and illustrates a new fungus (*Sclerotinia Panacis*) which is said to be the cause of a root-rot of ginseng; it was found near Apulia, N.Y.—A. B. RENDLE, E. G. BAKER, S. MOORE, and A. GEPP (Journ. Linn. Soc. Bot. **40**:1–245. *pls. 1–7.* 1911) have published an important paper entitled "A contribution to our knowledge of the Flora of Gazaland." The paper includes a general descriptive account of the country concerned, records about 1000 species of which approximately 180 are new to science. The plants were collected by Mr. C. F. M. SWYNNERTON and the types are deposited in the herbarium of the British Museum.—R. A. ROLFE (Bot. Mag. *t. 8417.* 1912) describes and illustrates a new species of *Stanhopea* (*S. peruviana*) from Peru, and (Kew Bull. 131–135. 1912) has published several new species of orchids including 4 from Panama and South America.—E. ROSENSTOCK (Rep. Sp. Nov. **10**:274–280. 1912) under the title "Filices costaricenses" has published 11 new species of ferns.—P. A. RYDBERG (Torreya **12**:1–11. 1912) in continuation of studies of the plants collected on the Peary arctic expeditions gives a list of the plants secured by Drs. WOLF and GOODSELL; the article includes a new species of *Conioselinum* (*C. pumilum* Rose) from Labrador. The same author (Bull. Torr. Bot. Club **39**:99–111. 1912) under "Studies on the Rocky Mountain flora XXVI" describes a new species in *Deschampsia* and one in *Anticlea*. Two new generic names are proposed, namely *Hesperochloa*, based on *Poa* (?) *Kingii* Wats., and *Dipterostemon*, based on *Brodiaea capitata* Benth.—C. S. SARGENT (Rep. Mo. Bot. Gard. **22**:67–83. 1911) under the heading "Crataegus in Missouri II" has described 14 new species.—A. K. SCHINDLER (Rep. Sp. Nov. **10**:403, 404. 1912) has published a new genus (*Kummerowia*) based on *Hedysarum striatum* Thunb. a species common to the New and Old World.—H. SCHINZ (Vierteljahrsschrift Naturf. Gesells. Zürich **56**:229–268. 1911) in an article "Beiträge zur Kenntnis der afrikanischen Flora" has proposed the following new genera belonging to the Amarantaceae: *Centemopsis*, *Nelsia*, *Neocentema*, and *Lopriorea*.—R. SCHLECTER (Rep. Sp. Nov. **10**:248–254, 291–296, 352–363, 385–397, 445–461. 1911–1912) under the title "Orchidaceae novae et criticae" has published about 70 new species of orchids from Central and

South America. One new genus (*Neokoehleria*) is included from Peru.—The same author (Orchis **6**:6–10. *pl. 1.* 1912) has published new species of orchids, 2 of which are from Colombia.—F. J. Seaver (Mycologia **4**:45–48. *pl. 57.* 1912) gives an account of the genus *Lamprospora* and adds 2 new species.—C. P. Smith (Muhlenbergia **7**:136–138. 1912) records a new variety of violet (*Viola Beckwithii* var. *cachensis*) from northern Utah.—O. Stapf (Hooker's Ic. IV, **10**: *t. 2947.* 1911) describes and illustrates a new genus (*Teonongia*) of the Moraceae from Tonkin; the same author (*ibid. tt. 2949, 2950*) describes and illustrates two new genera (*Lintonia* and *Dignathia*) of the Gramineae from British East Africa.—P. C. Standley (Proc. Biol. Soc. Wash. **24**:243–250. 1911) presents a synopsis of the American species of *Fagonia*, recognizing 12 species, 4 of which are new to science. The same author (Smith. Misc. Coll. **56**: no. 33. 1–3. 1912) has described 3 new species of flowering plants from Alberta, and (*ibid.* no. 34. 1–3. *pl. 1*) describes and illustrates a new species of *Viorna* (*V. Ridgwayi*) from southern Illinois.—F. Stephani (K. Sv. Vet. Akad. Handl. **46**: no. 9. 1–92. 1911) presents the results of an investigation of the Hepaticae collected on the Swedish expedition to Patagonia and Tierra del Fuego in 1907–1909; about 145 species are described as new to science. The types are deposited in the herbarium of the Botanical Museum at Upsala. The same author (Sp. Hep. **4**:641–736. 1911) continues his treatment of the Hepaticae and includes several new species from America belonging mainly to *Frullania* and *Archilejeunea*.—C. Torrend (Broteria Ser. Bot. **10**:29–49. 1912) under the title of "Deuxième contribution pour l'étude des champignons de l'ile de Madère" describes several species new to science and proposes a new genus (*Vermiculariopsis*) of the Sphaeropsidaceae. —W. Trelease (Rep. Mo. Bot. Gard. **22**:37–65. *pls. 18–72.* 1911) presents an illustrated account of the agaves of Lower California with a synopsis of the 25 reorganized species of which 17 are new to science; and (*ibid.* 85–97. *pls. 73–99*) gives a "Revision of the agaves of the group Applanatae," to which group 10 species are referred, 5 being hitherto undescribed; and (*ibid.* 99, 100. *pls. 100–103*) characterizes a new variety of *Agave* (*A. angustifolia* var. *Sargentii*) based on plants in cultivation at the Missouri Botanical Garden; and (*ibid.* 101–103. *pls. 104–108*) records 2 new species of *Yucca* from Texas and adjacent Mexico.—W. Wangerin (Rep. Sp. Nov. **10**:273. 1912) has published a new species of *Mastixia* (*M. philippinensis*) from the island of Luzon, P.I.— E. J. Welsford (Ann. Botany **26**:239–242. 1912) gives an account of an alga found in an aquarium associated with *Azolla caroliniana* which was imported from North Carolina. The author has given the alga the name of *Trichodiscus elegans*.—H. F. Wernham (Journ. Bot. **49**:317, 318. 1911) has published a new genus (*Pteridocalyx*) of the Rubiaceae from Demerara.—Different authors (Kew Bull. 35–44. 1912) have published several new species of flowering plants including 2 new species of *Columnea* from Guatemala and Venezuela, and a new *Zschokkea* from Peru; and (*ibid.* 90–107) under the title "Diagnoses

africanae XLVI" several new species are described, and the following new genera are proposed: *Isoberlinia* and *Paradaniellia* of the Leguminosae, and *Klaineanthus* and *Hamilcoa* of the Euphorbiaceae.—J. M. GREENMAN.

Recent work among Filicales.—DAVIS[23] has investigated the structure of *Peranema* and *Diacalpe*, Asiatic genera of ferns whose relationships have been somewhat doubtful. Both genera are polystelic; and while in *Peranema* the short-stalked sorus is a mixed one, with a receptacle of the Gradatae type and traces of a basipetal succession of sporangia, in *Diacalpe* the mixed sorus shows no traces of basipetal succession. Moreover, in *Peranema* the annulus is slightly oblique, while in *Diacalpe* it "is vertical in insertion, but slightly twisted in its course across the sporangial head." Both show relationships to species of *Nephrodium*, but are most nearly related to *Woodsia* and *Hypoderris*," and fall naturally into the Woodsieae-Woodsiinae group of Polypodiaceae," a group that is regarded as intermediate between Cyatheaceae and the Aspidieae. The conclusion is suggested that the *Aspidium* forms have come from a Gradatae ancestry, and "that *Peranema* and *Diacalpe* are relatively early members of a phyletic drift to the Polypodiaceae."

BOWER[24] has used a study of *Alsophila* (*Lophosoria*) *pruinata* as the basis for a discussion of an important phyletic sequence. *Lophosoria* is shown to be a more primitive type than the true species of *Alsophila* and worthy of generic separation from that genus. The phyletic relations with *Struthiopteris*, *Onoclea*, *Cystopteris*, *Acrophorus*, *Peranema*, *Diacalpe*, *Woodsia*, and *Hypoderris* are discussed and the following "progressions" announced: (1) the frequent dichotomous branching in Gleicheniaceae becomes rarer in the higher types, and the creeping axis of the earlier forms becomes ascending or erect in some of the later ones"; (2) "the peculiarities of the original gleicheniaceous type of leaf are shown in reminiscent details in the Cyatheaceae, but lost elsewhere"; (3) progression from primitive hairs to scales; (4) progression from the protostele of § MARTENSIA of *Gleichenia* to the solenostele of *G. pectinata* and *Lophosoria*, and the polystele of all other members of the series; (5) progression from the Simplices type of sorus (*Gleichenia* and *Lophosoria*) to the Gradatae type in Cyatheaceae, and finally to the Mixtae type in *Hypoderris*, *Peranema*, and *Diacalpe*, "a condition leading probably to that of the Aspidieae"; (6) progression from a larger spore-output and an oblique annulus to a smaller output and a vertical annulus; (7) progression from a larger sperm-output to a smaller one.

This series is believed by BOWER to constitute a true phylum, a phylum quite distinct from that of the ferns with originally marginal sori. The prob-

[23] DAVIS, R. C., The structure and affinities of *Peranema* and *Diacalpe*. Ann. Botany **26**: 245–268. *pls. 28, 29.* 1912.

[24] BOWER, F. O., Studies in the phylogeny of the Filicales. II. *Lophosoria*, and its relation to the Cyatheoideae and other ferns. Ann. Botany **26**: 269–323. *pls. 30–36.* 1912.

able phyletic sequence of families, therefore is as follows: "Gleicheniaceae, Cyatheaceae (with minor groups, e.g., Woodsieae, etc.), Aspidieae."

Miss HUME[25] has investigated the sieve tubes of *Pteridium aquilinum*, and compared them with those of *Lygodium dichotomum* and *Marsilia quadrifolia*. The xylem has long received intensive study on account of its service in conclusions concerning phylogeny; but there are symptoms that the phloem is now beginning to come into its own. The stock contrasts between the sieve tubes of pteridophytes and spermatophytes are now beginning to break down and Miss HUME has contributed her share to this process. Not only does callus appear, as RUSSOW showed, but the author shows that the pores are not closed. "The outstanding differences are in shape and contents; the sieve tubes of vascular cryptogams are larger and thicker walled and contain refringent granules." The larger size and thicker walls are thought to be associated with the fact that the sieve tubes of pteridophytes (on account of the absence of secondary thickening) have to function for a long time, in some cases for as much as 20 years, while in some dicotyledons and gymnosperms they are renewed each year. The time is at hand when the sieve tubes can be linked up in phyletic sequences as the xylem elements have been.

THOMAS[26] has discovered in the Jurassic of Yorkshire sporangia of *Coniopteris hymenophylloides* Brongn. and *Todites Williamsoni* Brongn., which support the view that the former species is closely related to the modern Cyatheaceae, and which furnish for the latter species additional points of resemblance to the modern *Todea*. Fertile material of *Cladophlebis lobifolia* Phill. was also secured, which justifies its removal from the form-genus and its provisional placing in a new genus *Eboracia*, related in sori and spores to *Coniopteris*, but very distinct in the form of the fertile fronds.—J. M. C.

American cecidology.—All students of the biological sciences will be interested in the increased attention which cecidology is receiving in America, and also in the fact that it is being studied by both entomologists and botanists. FELT presents four papers. In the first[27] he gives a very complete list of plants on which the cecidia of our American gall midges are known to occur and the names of the gall-makers. Our knowledge of this group of gall-makers is very indefinite, and therefore the very brief one-line descriptions may appear unsatisfactory to many who are unfamiliar with the subject. However, the list will prove of very great value to the student of plant pathology and cecidology. In a second paper[28] FELT describes 17 new species of gall midges,

[25] HUME, E. M. MARGARET, The history of the sieve tubes of *Pteridium aquilinum*, with some notes on *Marsilia quadrifolia* and *Lygodium dichotomum*. Ann. Botany **26**:573–587. *pls. 54, 55*. 1912.

[26] THOMAS, H. HAMSHAW, On the spores of some Jurassic ferns. Proc. Cambridge Phil. Soc. **16**:384–388. *pl. 3*. 1911.

[27] FELT, E. P., Hosts and galls of American midges. Jour. Econ. Entomology **4**:451–475. 1911.

[28] ———, New species of gall midges. *Ibid.* **4**:476–484. 1911.

but many of them are not true gall-makers while others produce very small and insignificant galls. In a third paper[29] the same author describes three new species of dipterous gall-makers, and in the fourth[30] he describes four new species of gall midges from St. Vincent, West Indies. The development and structural characters of all these galls remains to be worked out by the botanist.

BEUTENMÜLLER[31] has given us another most excellent paper on the North American galls. This last paper is on the genus *Dryophanta*, and contains excellent descriptions of both galls and insects of the 39 known species, with complete synonomy and bibliography. Most of the galls are figured, and all of them occur on oaks, but in a few cases the specific name of the host is not known. The 32 species for which the hosts are given are found on 24 species of oak. *Quercus rubra* leads with 7 species, *Q. alba* has 5, *Q. coccinea* has 4, *Q. undulata*, *Q. velutina*, and *Q. nana* have 3 each, *Q. arizonica*, *Q. marylandica*, *Q. prinoides*, *Q. palustris*, and *Q. laurifolia* have 2 each. *Dryophanta palustris* is found upon 7 different hosts, *D. lanata* on 5, *D. notha* on 3, 5 other species on 2 each, and 24 species on 1 each.

The same author[32] also describes and figures two new species of *Holcaspis* galls from Mexico. These papers will be absolutely necessary for students who wish to make botanical studies of cecidia.

One of the most interesting and important contributions to American cecidology is by ERWIN F. SMITH,[33] who has continued his studies on crown gall of plants, and presents some interesting comparisons with the cancer of human beings. The similarity between plant and animal malformations has attracted the attention of many observers, who have looked upon the study of plant galls as a fruitful field of investigation, but unfortunately very few have gone into it far enough to see the real possibilities. SMITH's confidence in this line of work is expressed as follows: "I believe we have in these particular plant overgrowths a key to unlock the whole cancer situation. In consideration of these discoveries many closed doors in cancer research must now be opened, and studies on the etiology of the disease must be done over with a view to finding a parasite within the cancer cell, and separating it therefrom by an improved technic of isolation." In answer to his critics he claims that the crown gall is not the same as a granulomata of the animal. He also shows that the tendency of the human cancer to form secondary growths by means of strands of tissue is similar to the formation of secondary growth

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[29] FELT, E. P., Three new gall midges. Jour. N.Y. Entom. Soc. **19**:190–193. 1911.

[30] ———, New West Indian gall midges. Entomol. News **23**:173–175. 1912.

[31] BEUTENMÜLLER, WILLIAM, The North American species of *Dryophanta* and their galls. Amer. Mus. Nat. Hist. **30**:343–369. 1911.

[32] ———, Two new species of *Holcaspis* from Mexico. Psyche **18**:86, 87. 1912.

[33] SMITH, ERWIN F., On some resemblances of crown gall to human cancer. Science N.S. **35**:161–172. 1912.

of the crown gall, and believes that "we have in the crown gall a striking analogy to what occurs in malignant animal tumors." He does not claim that the animal cancer and crown gall are due to the same organism. The latter part of the paper is devoted to physiological characters of the organisms and presents some suggestions which will be of importance to the plant physiologist who has the courage to attempt to explain the formation of plant cecidia as a result of irritation by parasitic fungi and insects.—MEL T. COOK.

Inheritance in flax.—TAMMES[34] has studied a number of characters in crosses between two varieties of the common flax (*Linum usitatissimum*) and between these and *L. crepitans* and *L. angustifolium*. She has dealt quantitatively with the length of seeds, length and breadth of petals, color of the flowers, degree of opening of the mature capsules, and the hairiness of the dissepiments of the capsules. Hairiness of the capsules and the lightest blue color of the flowers are each determined by a single Mendelian gene, but all the other characters are obviously more complex. The author believes that all of these characters are likewise determined by genes which segregate normally in the F_2, though they cannot be followed individually because several genes affect the same characteristic and act together in such a way that the grade of development of the character depends approximately on the number of these genes present. This results in a continuous series of gradations which are superficially indistinguishable from fluctuations, but which differ by being inheritable. Several evidences for the correctness of this interpretation are reported: The F_1 is in each case intermediate between the parents and no more variable than they; in the F_2 the variability is considerably increased, and the curves stretch out toward those of either parent, but frequently fail to reach them owing to the small size of the families investigated; when F_3 families are grown from the extreme variants of the F_2, a still closer approach to one or the other P_1 results, apparent identity with the parental type being attained in several cases. From the proportion of F_2 and F_3 families which approached in any given characteristic the condition of the P_1 generation, Miss TAMMES estimates the number of genes probably involved in differentiating the two parental types in each cross with respect to the several characteristics studied. She concludes that in length of seeds not less than four differentiating genes were involved in every cross made, in some crosses certainly a still larger number. In width of petals the simplest cross must have had differences between the parents in 3 or 4 genes, and the other crosses a considerably higher number. In flower-color different intensities of blue were apparently dependent on three genes. Between capsules which remain closed at maturity and those that spring wide open, 3 or 4 genes are involved. Later generations will be needed fully to test these conclusions.—GEO. H. SHULL.

[34] TAMMES, T., Das Verhalten fluktuierend variierender Merkmale bei der Bastardierung. Recueil Trav. Bot. Neerlandais **8**:201–288. *pls.* 3–5. 1911.

Beach vegetation.—A detailed ecological study of the beach vegetation of that portion of the shores of Lake Michigan which extends from Waukegan, Illinois, to Kenosha, Wisconsin, has recently been made by GATES.[35] Unfortunately it contains little in the way of quantitative data upon the various factors involved, but as a record of the vegetation of this region it is an admirable and valuable contribution.

The lack of any definitely fixed conception of what constitutes the unit of vegetation known as a "plant association" is shown not only by the author's review of the literature upon the subject, but also by his subdivision of the vegetation of the very limited area under investigation into more than fifty different associations. Such a multiplication of associations indicates a danger of making the segregation upon a floristic rather than an ecological basis, and also points to the need of some well recognized subdivision of the association, and yet, even with the most conservative treatment, it is to be expected that a region such as this, representing as it does the meeting place of the northern conifer, the eastern deciduous, and the prairie plant provinces, would present an unusual number of vegetational types. The genetic relationship of these various associations is clearly indicated and exhaustive lists of species are given.—GEO. D. FULLER.

The black oaks.—At the meeting of the American Philosophical Society (Philadelphia) on April 19, 1912, Dr. TRELEASE discussed the classification of the black oaks. The abstract of his paper is as follows: Attention to bud and fruit characters has led to a classification of the black oaks quite different from their usual arrangement according to leaf-form, and five groups of species are recognized, three of the Eastern states, one of the Southwest, and one of the Pacific states. The eastern groups are the black oaks (black jack, turkey oak, Spanish oak, and quercitron), scarlet oaks (scarlet oak, gray oak, Hill's oak, red oak, Texas red oak, and bear oak), and swamp oaks, these of two sets, the water oaks (water oak, pin oak, and Stone Mountain oak) and willow oaks (shingle oak, willow oak, laurel oak, running oak, cinnamon oak, and myrtle oak). The Southwestern olive oaks (Emory's oak and the white-leaf oak) and the Californian holly oaks (evergreen oak, Highland oak, and Kellogg's oak) are less related to one another and to the eastern black oaks than these are to one another, and appear to have originated independently of them.

Nuclear phenomena in the Uredineae.—WEIR[36] has published a brief summary of the outstanding features of the Uredineae, which will be of service to those who wish a condensed outline of the nuclear conditions in the various stages of the life history of rusts.—J. M. C.

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[35] GATES, FRANK C., The vegetation of the beach area in northeastern Illinois and southeastern Wisconsin. Illinois State Lab. Nat. Hist. **9**:255–272. *pls. 37–56.* 1912.

[36] WEIR, JAMES R., A short review of the general characteristics and cytological phenomena of the Uredineae, with notes on a variation in the promycelium of *Coleosporium Pulsatillae* (Str.). New Phytol. **11**:129–139. 1912.

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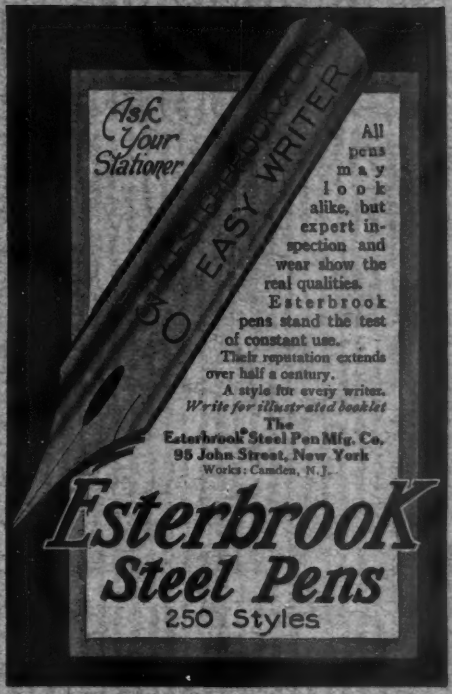
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